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A REVIEW OF STUDIES ON THE MEXICAN FRUITFLY AND RELATED MEXICAN SPECIES

BY

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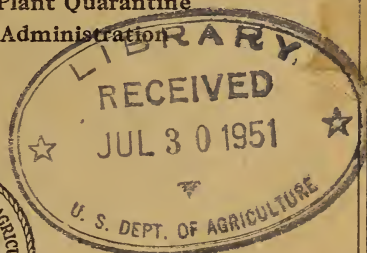W. E. STONE, Senior Entomologist
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INTRODUCTION

Fruitflies have received this name because the larvae develop within the pulp of fruits, causing them to become wormy. Some species attack only wild fruits of little economic importance, while others attack cultivated varieties, thereby causing heavy financial loss. It is with flies of the second type that this publication is concerned.

In Mexico there are several species of fruitflies of economic importance, but the one responsible for the greatest loss is *Anastrepha ludens* (Loew),[2] commonly called the Mexican fruitfly. It attacks among other things two important crops, citrus and mango. Because of its importance this species will be discussed first.

The Mexican fruitfly, occurring as it does in large numbers in northeastern Mexico, annually threatens the citrus plantings along the Rio Grande in Texas, and its spread into other regions in the United States is a matter of concern.

NATURE OF THE DAMAGE CAUSED BY THE MEXICAN FRUITFLY

The attack on the fruit is made by the adult female. She pricks the skin with a sharp, bladelike ovipositor and deposits her eggs beneath it. When these eggs hatch, the surviving larvae grow, burrow deeply throughout the flesh of the fruit, and ruin it. When they become mature they leave the fruit, which by that time has usually fallen, crawl a short distance into the soil, and there pupate. From the resulting puparia adult flies emerge and work their way to the surface.[3]

The indication of infestation differs in various fruits. Infested grapefruit is often a deeper, somewhat golden color. This is especially noticeable early in the season, before the crop as a whole has become well colored. There is sometimes in the infested fruit a small opening, or exit hole, through which larvae can be seen crawling and falling to the ground while the fruit is still on the tree. Around this small hole there may be a soft, plainly marked area, as seen in figure 1, or the small opening may show no differentiated area. In Marsh (Marsh Seedless), one of the varieties of grapefruit most commonly grown, the larvae usually work first in the central core of the fruit and from there outward, until they have destroyed much of the pulp.

Infested mangoes are shown in plate 1.   The lower fruit (pl. 1, *B*) is from Cuernavaca in the State of Morelos, a short distance south of Mexico City.   In some of the gardens there nearly all mangoes become infested.

NATIVE HOME OF THE MEXICAN FRUITFLY

Anastrepha ludens is a native insect.   Citrus and mango, the two crops it chiefly attacks, were introduced into America.   Evidently, therefore, it adopted these in preference to some native host in which it had lived before their introduction.   It has been customary to speak of the insect as a tropical one, and those who have written regarding it have assumed that its original home was in southern Mexico, probably in the State of Morelos, because of the fact that it causes heavy damage in Cuernavaca and surrounding municipalities.   It has therefore been called the "Morelos orange fruit-worm" (*36*).[4]   The

FIGURE 1.—Grapefruit showing an exit hole of a larva of *Anastrepha ludens* and the soft area surrounding it.

opinion that *A. ludens* is a tropical insect and that it originated in southern Mexico is, however, a questionable one.

It may be assumed that, since it has adopted citrus and the common mango, the insect originally lived in something related either to the one or to the other.   It is the common, or "corriente," mango that is most heavily attacked.   In some areas, however, where the fly is generally distributed, mangoes are very little attacked, whereas citrus is commonly so.

The mango (*Mangifera indica* L.) is a tree of the family Anacar-

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[4] Italic numbers in parentheses refer to Literature Cited, p. 149.

diaceae and is of East Indian origin. Certain other fruits of this family are native to Mexico. The most familiar are the species of *Spondias* known locally as ciruela, and in English as mombin, hobo, or hog plum. Another fruit belongs to the genus *Cyrtocarpa*, and is known as berracos and chupandías, while still another, *Anacardium occidentale* L., is called cashew, or cashew nut, in English. These, a few others, and many plants related to the poison ivy constitute the Mexican list. But these fruits, although some are ideal for fruitflies, are not attacked by *Anastrepha ludens*. Some of them are attacked by another fruitfly, a tropical species which in this publication will be called Mexican *Anastrepha mombinpraeoptans*.

It is true that in rearing many thousands of this form from *Spondias* an occasional *Anastrepha ludens* may be found, but this is exceedingly rare. The fruit is not normally a native host. On the other hand, in Puerto Rico true *A. mombinpraeoptans* Seín is common to both mango and *Spondias*, but not to citrus, and W. A. McCubbin[5] there found it also in cashew nut, a third member of the family. *A. mombinpraeoptans*, therefore, in striking contrast to *A. ludens*, is a tropical insect associated with the Anacardiaceae.

There are various native trees in Mexico belonging to the citrus family. Some of them produce very small fruits; others, fruits that are dry and not suitable for fruitflies. A few, however, have fruits which are ideal as hosts. Such fruits are known in Mexico as zapotes or chapotes or limoncillos, the last name being due to the fragrant oils they contain, much like the oils of citrus. They are also called naranjillos after "naranja," the name for the orange.

One of these native fruits, the yellow chapote (*Sargentia greggii* S. Wats.), is distributed throughout Tamaulipas, Nuevo León, and San Luis Potosí, and, as will be discussed later in detail, it is there very widely infested by *Anastrepha ludens* in its native habitat. Large numbers of larvae of *A. ludens* live in this native fruit, and after pupation and emergence have occurred the adults spread out on the wing to cover a wide area. A considerable series of parasites attack the insect in this native environment, a fact indicating long association. As will be shown later, *A. ludens* also can well withstand freezing weather, whereas in hot areas it may be killed by the heat of the sun.

In southern Mexico this widely used native host, *Sargentia*, does not exist. White sapote, another member of the citrus family, occurs in small numbers in Cuernavaca and is heavily infested. But it is there a cultivated tree, its natural range, according to Standley (*38, p. 527*), being from Sonora to Jalisco, and while *Anastrepha ludens* now occurs in Jalisco it has not yet reached the citrus plantings in Sonora. It has never occupied the native range of the white sapote. There is, so far as the authors know, no widespread native reservoir around Cuernavaca, as there is in northeastern Mexico.

Moreover, the old inhabitants in Morelos have been credited with the statement that in the early days both citrus and mango were free of the pest. Santillan, in Herrera et al. (*21, p. 8*), writing in 1900, stated that the oldest inhabitants in Yautepec at that time said that the insect was imported into that municipality from Cuernavaca 60 years before.

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[5] Personal communication.
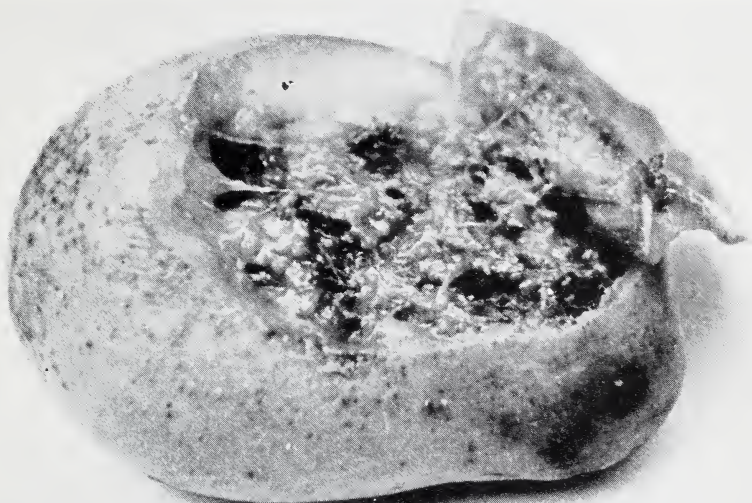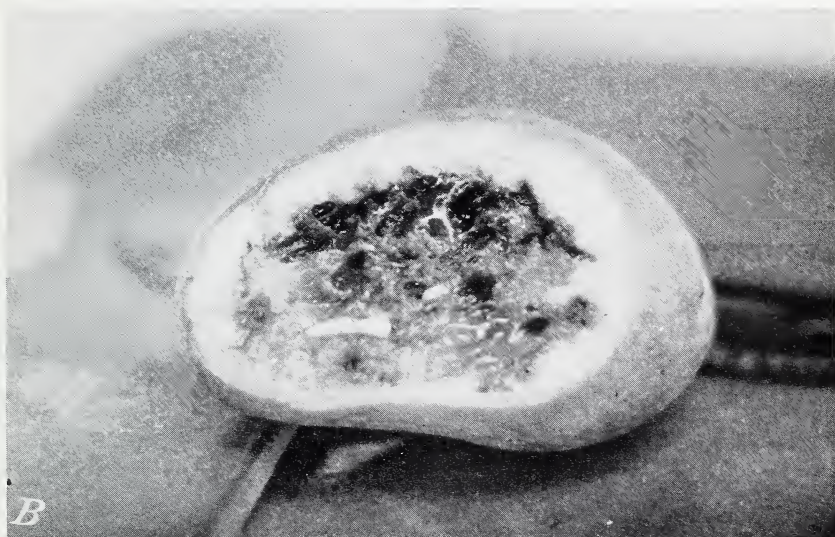
EFFECT ON MANGO OF INFESTATION BY LARVAE OF ANASTREPHA LUDENS

A, Stringy consistency of pulp often following the feeding by the maggots; *B*, more common result of the feeding by the maggots.
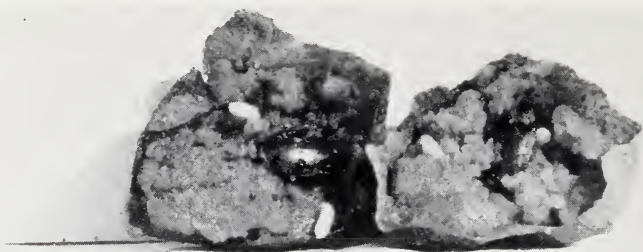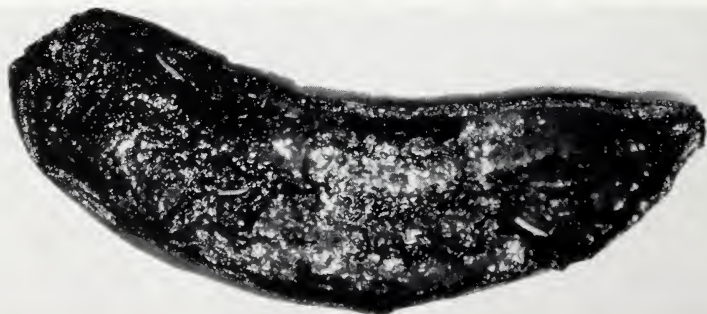
NATURE OF INJURY TO FRUITS CAUSED BY LARVAE OF ANASTREPHA LUDENS
A, to sapodilla; B, to mammee apple; C, to peach; D, to banana.

All this indicates that *Anastrepha ludens* is not a native of that southern region. Introduced there and finding no abundant supply of native hosts, it would quite naturally adopt crops as its only source of survival and would, in a short time, attract attention as an economic pest. In its native home it would not be forced to this necessity and its adoption of citrus would be more gradual and less spectacular. If oranges were less enjoyed than its native host, the attack upon them would be light, and only with unusual conditions like the planting of large quantities of grapefruit, a very favored host, would its desertion of its native food become outstanding and strikingly noticeable.

All available data indicate, therefore, (1) that the native home of *Anastrepha ludens* is the northeastern section of Mexico, a section widely occupied by a native host, *Sargentia greggii*, a close relative of *Citrus;* (2) that it still lives, as it has always lived, widely distributed in its native habitat; (3) that in this area it adopts varieties of *Citrus*, depending on their relative attraction for it in relation to that of its native host; and (4) that, transported to other regions lacking a wide distribution of its native host in which to survive, it becomes at once a conspicuous pest of cultivated crops.

There appears no reason, therefore, as is commonly done, to attempt to explain on the basis of climate why the insect has spread over the northeastern section of Mexico and why it has not succeeded in doing so on the west coast. In the east it has always existed. In the west it has been forced to wait on artificial carriage by man or on gradual dissemination, the manner by which it has been spread through so much of the Mexican Republic. When a few years ago it was found in Culiacán, Sinaloa, its northernmost point to date on the west coast, it was found there feeding in white sapote.

For the United States this story has a definite meaning. Light infestations in the insects' native home, as, for example, in oranges in Nuevo León, are not due to climatic depression. They represent the situation so commonly found with native insects. On the other hand, introductions into new areas lacking all the associations of natural environment have resulted commonly in Mexico in abundant attack on cultivated crops. There is little reason to suppose that a similar attack would not occur in grapefruit plantings in certain regions in the United States. Heavy infestation may be expected.

FRUITS ATTACKED BY THE MEXICAN FRUITFLY IN NATURE

The fruits which *Anastrepha ludens* attacks may be divided into two groups, the first group comprising those that have been found infested by the fly in the field and the second comprising those in which the fly readily oviposits and in which the larvae readily mature, but which have not been found infested in nature. With some of these, of course, infestation in nature would be impossible because they are not grown within the present range of the fly. A knowledge of their suitability as hosts is valuable, however, because the fly at any time may gain access to regions producing such fruit. Other artificial hosts not found infested in nature although they occur in areas occupied by the fly are instructive in that they show the kinds of environment avoided by the insect and point the way to studies in proof of its habits. In the following list a rather detailed discussion will be given under each host.

It will be well at the outset to clarify certain references. Mackie (*25, p. 308*) reported information from Zetek to the effect that *Anastrepha ludens* had been taken in the Canal Zone feeding in a cucurbit, *Gurania suberosa* Standl., and that Singleton (in the Canal Zone) had found it feeding in a legume called guinguiles, or "jinicuila." *A. ludens* does not occur in the Canal Zone, and the species mentioned by Zetek, which was at the time determined by the taxonomists as *A. ludens*, is a tropical species with quite different biology. As will be discussed presently, jinicuil is the name used for *Inga jinicuil* Schlecht., a tree of the mimosa family, the pods of which are the major host of another species, *A. distincta* Greene. In Mexico *A. ludens* very seldom uses these pods and, being absent from the Canal Zone, could not utilize *Inga* pods there. The references associated with *Inga* in the Zone, therefore, refer to *A. distincta*.

Dampf's citation of huicochote, or huaxocote, as a host in 1928 (Mackie (*25, p. 308*)) may have referred to the record of De la Barreda in his report for September 30, 1900 (*21, p. 41*). In Morelos, where he found the infestation, *Malpighia glabra* L. is referred to as huaxocote (*30, p. 321*). Stone has exposed huaxocote fruits to populations of *Anastrepha ludens* without infestation resulting, but this does not prove that field infestation may not occur.

Achras zapota L.

The sapodilla (*Achras zapota* L.) is the species called the chicozapote in Mexico, from the trees of which chicle is obtained for chewing gum. The fruit is highly esteemed and was early reported as infested by *Anastrepha ludens*. It is one of the hosts listed by Crawford (*7, p. 461*).

Although the authors have not found the sapodilla infested in nature, the fruit has been heavily attacked under laboratory conditions. In this work Stone [6] found that adult flies seldom infested ripe sapodillas, but that when green ones were exposed infestation readily resulted. The fruit, when attacked, breaks down much as do peaches. This condition is shown in plate 2, *A*. Plate 5, *E*, shows the interesting type of package in which chicozapotes are sold in Mexico.

Annona spp.

In Mexico there are a dozen or more species of *Annona*, both wild and cultivated, of which the best known in the United States are the cherimoya (*A. cherimola* Mill.), the custard apple (*A. reticulata* L.), and the soursop (*A. muricata* L.). The authors have no record of infestation of the soursop, but both the cherimoya and the annona, or custard apple, are attacked by *Anastrepha ludens*. Skwarra [7] raised two males from cherimoya purchased in Mexico City, and these fruits so infested have been taken at quarantine.

Mann [8] while in Guadalajara, purchased a lot of annonas, said to have come from Colima, which were heavily infested, and when adults were reared they proved to be *Anastrepha ludens*. He was inclined to believe the annona as acceptable as the grapefruit, putting these two fruits after sour orange.

[6] See manuscript report 57, p. 154.
[7] See manuscript report 24, p. 153.
[8] See manuscript reports 1, 2, p. 152.

Casimiroa edulis Llave and Lex.

White sapote (*Casimiroa edulis* Llave and Lex.), known generally in Mexico as zapote blanco, may represent both *C. edulis* and *C. sapota* Oerst. According to Standley (*38, p. 527*), *C. edulis* is native to the west coast of Mexico, whereas *C. sapota* extends to San Luis Potosí and Querétaro. In any case, the common market white sapote is cultivated in small numbers in Cuernavaca and is there very heavily infested by *Anastrepha ludens*, as it is also in Santa Engracia. It is one of the two native fruits of the citrus family that is so attacked. Advice from native sources indicates that in parts of Jalisco it is impossible to leave the fruit on the trees because of infestation and that it is gathered green for this reason.

In the early summer of 1933, through the courtesy of the Mexican Department of Agriculture,[9] flies from white sapote were received from the vicinity of Culiacán on the west coast. These all proved to be *Anastrepha ludens* and constituted the most northern record for the species in the western region.

Citrus aurantium L.

The sour orange (*Citrus aurantium* L.) is one of the favorite hosts of *Anastrepha ludens* and has been found infested in almost every place where the fly occurs and the fruit is grown in quantity. It was one of the fruits commonly infested when the fly was found in the Rio Grande Valley of Texas in 1927, and sour orange trees were removed from groves in an effort toward fly elimination. The fact that sour orange is not gathered as a crop, but is usually grown only for seed, and so is often left on the trees for considerable periods, no doubt increases the possibility of infestation. Field-infested fruits present the appearance indicated in plate 3, *A*.

Several people have expressed the opinion that sour orange is the most attractive fruit. Mann,[10] after visiting Jalisco and interior sections of Mexico, placed the hosts in the following order of preference: Mango, sour orange, annona, and grapefruit. Skwarra[11] places the sour orange first in many sections, after visiting much of the territory covered by Mann. Grapefruit, however, is often more heavily attacked than sour orange. This subject as a whole will be discussed somewhat later (p. 22).

Citrus grandis Osbeck

The grapefruit and the shaddock, which the botanists include under *Citrus grandis*, are both grown in Mexico. In some of the small towns on the road to the Pacific from Mexico City shaddocks are offered for sale at road stands. Plummer found infestations in such shaddocks and in the fruits of a tree at El Carmen, Tamaulipas.

The grapefruit is probably the most heavily attacked of any cultivated fruit, with the possible exception of the common mango. In Santa Engracia entire grapefruit crops are sometimes lost, while

[9] See manuscript report 43, p. 153.
[10] See manuscript report 2, p. 152.
[11] See manuscript report 24, p. 153.

mangoes there are very slightly attacked, a situation rather different from that in Cuernavaca.

All varieties of grapefruit are attacked, but the early maturing ones suffer first. Plate 4, *A*, shows the earliest appearance of infestation, which is usually at the blossom end. Small dark, or brownish, lines traverse the rag. These then become more extensive, holes may be seen throughout the rag, and full-grown larvae are found in the center of the fruit, as seen in plate 4, *B*. When the stem end of the fruit is attacked, it may appear as depicted in plate 4, *C*. A random collection of fruit from under an infested tree is shown in plate 3, *C*. Since in Mexico local grapefruit crops are sometimes lost, there is no question that *Anastrepha ludens* is a serious menace to grapefruit production. In Texas, infestation in the grapefruit crop of 1936–37 was sufficiently severe to show this fruitfly's possibilities.

Citrus nobilis Lour.

Kid-glove oranges of the mandarin and satsuma types are grown in Mexico, and these are attacked to some extent. No special study has been made of these fruits in relation to infestation in general, since they are not largely grown in areas where studies have been made. Stone has shown, however, that the larvae require much longer to develop in mandarins than in most other fruits. Skwarra [12] found these fruits infested along with other citrus in the gardens in the State of Oaxaca. Tangerines have been infested in cages, but very slightly.

Citrus sinensis Osbeck

Of the sweet orange varieties the navels in Santa Engracia have been the most heavily infested, the loss in 1935 being estimated by the grove manager at 25 percent. This is in marked contrast to the condition found by Mann,[13] who considered infestation in navels at Pueblo Viejo near Tampico very unusual, and who found the navel orange in Jalisco, along with sweet seedlings,[14] to be among the last of the fruits infested. Skwarra [15] found "California oranges" infested in the gardens of Oaxaca during November.

While all varieties are infested, the degree of infestation appears to be largely associated with the date of maturity, those oranges that ripen late in the year escaping a considerable degree of the infestation found in the earlier maturing varieties. At Santa Engracia the navels are the first to mature. When infested they turn a rich orange color, but may otherwise appear sound until cut open, when they show the characteristic feeding in the interior (pl. 3, *B*).

Citrus spp. (limes and lemons)

Some confusion exists because of the fact that what are called limes in the United States are called limónes (lemons) in Mexico. The sweet limes known as limas in Mexico are not grown in the United States.

[12] See manuscript report 7, p. 152.
[13] See manuscript report 1, p. 152.
[14] See manuscript report 2, p. 152.
[15] See manuscript report 7, p. 152.
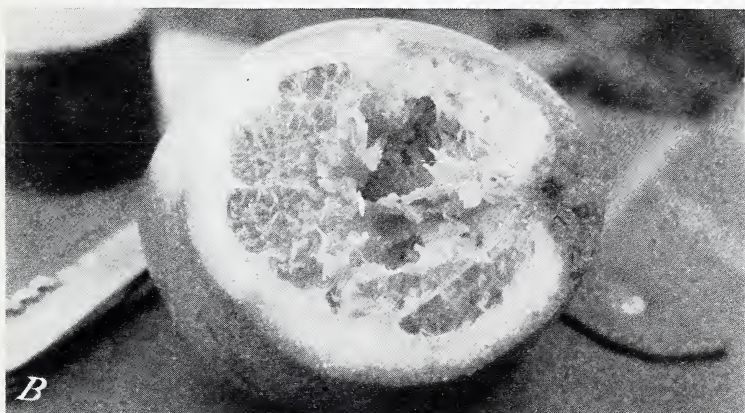
EFFECTS OF INFESTATION IN CITRUS FRUITS BY LARVAE OF ANASTREPHA LUDENS

A, Injury to sour orange; *B*, injury to navel orange; *C*, grapefruit collected under a single tree showing degrees of infestation by the maggots.
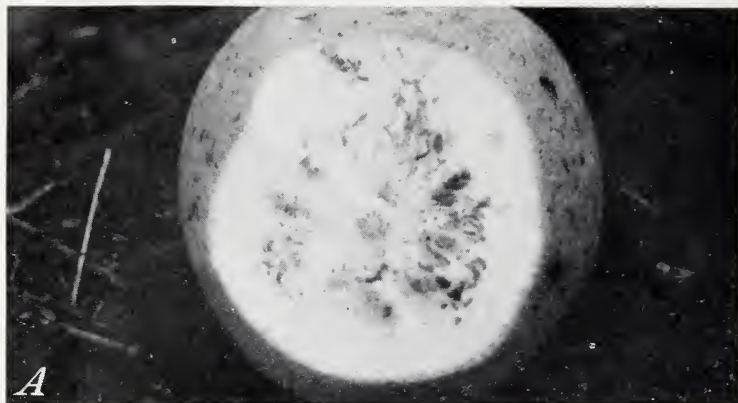
STAGES OF INFESTATION IN GRAPEFRUIT BY LARVAE OF ANASTREPHA LUDENS

A, Soon after attack; *B*, more advanced infestation; *C*, heavy infestation at the stem end.

The small fruit, known as lima chica, is very abundantly infested. It is somewhat depressed from both ends, and possesses a prominent nipple situated in a depression. A larger fruit, very similar to this, grown under the name of lima grande, is also infested. A third form, grown considerably in the west, has a less prominent nipple with very little depression surrounding it. This is called lima chichona. All these fruits are somewhat similar in shape, not elongate, and are easily distinguished as limas. Another form is known as lima naranja. It has much the shape and color of a seedling orange, has something of that odor, and has a nipple suggestive of that on a lemon. The authors have had no field experience with the last two forms and are unable to give definite evidence regarding the question of their infestation.

All these fruits are low in acid and are eaten out of hand, although sour varieties also occur. They are here classed under the species *Citrus aurantifolia* (Christm.) Swingle.

Distinct from these fruits are those which are typically shaped like a lemon and are grouped here as *Citrus limonia* Osbeck. The small, sour fruit known in the United States as the Mexican lime is the most common. Under this same name, limón agrio in Mexico, are also grouped several larger fruits similar to the cultivated varieties of limes grown in the United States. The fruit known in the United States as lemon and in Mexico as limón del extranjero might also be included in the group. None of these fruits has been found infested.

There occurs also in Mexico a fruit in every way externally resembling a lemon, which is sweet in taste and which is referred to as limón dulce. Sometimes this possesses a thin skin, but very often the skin is thick like that of a citron. The fruit is infested.

In addition to the fruits discussed, the citron is grown in a number of forms. It is commonly called cidra, or cidra limón. So far as the authors know, it is free from attack. Some of the lemon-shaped fruits are undoubtedly citrons. These fruits are here grouped as *Citrus medica* L., and have not been found infested.

Eugenia jambos L.

The rose apple (*Eugenia jambos* L.), which is a native of southeastern Asia and Australia, is sometimes cultivated in Mexico in considerable numbers. Near Cordoba, Veracruz, and on the Isthmus road the fruits are very heavily infested by Mexican *Anastrepha mombinpraeoptans* and Mexican *A. fraterculus*. Only a few trees occur in Cuernavaca, and these had been under observation for several years before an infestation by *A. ludens* was reported by Stone.[16] Previous to that time he had exposed rose apples to mated adults of *A. ludens* in the laboratory and had obtained ample artificial infestation.

Inga jinicuil Schlecht.

The tree called jinicuil in Morelos is grown to some extent there for coffee shade. It grows to be large and the pods are a foot or more in length and about an inch thick. These pods are an article of commerce, since the sweet pulp between the seeds is eaten. They are the host of *Anastrepha distincta* in this area, and many larvae may be

[16] See manuscript report 49, p. 153.

found feeding in them. In 1932, however, Plummer [17] reared *A. ludens* from field-infested *Inga* pods in Cuernavaca, and thus demonstrated that this fruit serves as a host of the Mexican fruitfly. Since that date some numbers have been reared along with the populations of *A. distincta*, but *Inga* pods apparently are only a casual host of *A. ludens*.

MAMMEA AMERICANA L.

The mammee apple (*Mammea americana* L.) is not extensively grown in the areas occupied by *Anastrepha ludens*. The common mamey of Mexico (*Calocarpum mammosum* (L.) Pierre), not infrequently called the zapote mamey, is quite a different fruit and is the major host in Morelos of *A. serpentina* (Wied.). This fruit is elongate (pl. 5, *D*), whereas the mammee apple (pl. 5, *C*) is almost spherical. Because the latter fruit is introduced, it is called zapote de Santo Domingo in Mexico to distinguish it from the common mamey.

The only infestation of the mammee apple by *Anastrepha ludens* that has come to the authors' attention is that existing in Coatlán del Río, Morelos, reported by Stone.[18] The larvae make rather definite burrows through the flesh, which darkens in the infested region, as may be seen in plate 2, *B*, which shows a field-infested fruit from that region. In the early literature on the fruitfly, infestation of mamey by *A. ludens* is referred to, but in all probability these references are concerned with *A. serpentina* in the zapote mamey.

MANGIFERA INDICA L.

The mango (*Mangifera indica* L.) is known by the same name both in the United States and in Mexico. It is a native of Asia and is cultivated extensively in Mexico, where it was early introduced, probably into the State of Veracruz. There are several types, among which the common Mexican mango is distinguished by a definite turpentine odor. These fruits presumably are seedlings, as they vary greatly in size, shape, and character. Individual trees differ definitely from others in their fruiting seasons.

These common mangoes are one of the favorite hosts of *Anastrepha ludens*. In some regions infestation is very heavy. Bliss and McPhail [19] state that in Cuernavaca infestation commonly exceeds 90 percent, and in the drops used by them extensively as a source of material they had no record of finding a single one uninfested.

When attacked by the larvae, the interior of the fruit may remain more or less unaltered except for the results of feeding, or it may become quite soft and stringy, as shown in plate 1, *A*, a condition due, probably, to inoculation with microorganisms.

The classification of the mango in Mexico appears to be in a very unsatisfactory state. There are, however, several very definite horticultural varieties. One of the better known is a yellow fruit called the Manila mango. It has been asserted by many that this variety is free from attack by *Anastrepha ludens* but this is not the case. At Temisco, Morelos, Plummer [20] [21] examined 27 mangoes classed as Ma-

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[17] See manuscript report 40, p. 153.
[18] See manuscript report 59, p. 154.
[19] See manuscript report 8, p. 152.
[20] See manuscript report 31, p. 153.
[21] See manuscript report 32, p. 153.

nilas and found 366 larvae in the 27 fruits.   Stone and Plummer [22] found common mangoes and Manilas growing together at El Potrero, Veracruz, at an altitude of 1,200 feet.   Practically all the drops of the common mango were infested, whereas only 3 Manilas out of 50 examined under half a dozen trees showed any infestation.   This gives support to the idea that Manilas are less abundantly attacked.

Through the kindness of Dyfrig McH. Forbes, of El Potrero, the following tabulation made by him in 1937 can be included.   He observed fruits from 6 Manila mango trees in each of 7 localities, 2 boxes of 200 mangoes from each.   By careful inspection he arrived at the following infestation figures for each location:

Location:	Percent infested
Potrero Viejo	34
El Suchil	17
Concepción	41
San Lorenzo	27
San Francisco de las Mesillas	23
San José del Corral	28
La Pesca	12

According to Forbes' recollection, cases of infestation in Manilas had been seen the previous year, but infestation was thought to have been not greater than 3 to 5 percent.

In the west of Mexico *Anastrepha ludens* is only beginning to appear, so that there has been no opportunity to determine the natural reaction of *A. ludens* to the large mangoes grown at El Dorado, Sinaloa.   An extensive variety planting of mangoes from India occurs there.   Some of these were shipped to the laboratory, and Stone [23] exposed them to flies from two sources, (1) from the common mango in Cuernavaca, and (2) from white sapote from Nayarit.   In the first test there proved to be 1,021 larvae in one mango exposed to the flies from Cuernavaca and only 53 in one exposed to flies from the white sapote.   In a second test the difference was not so striking, there being 73 larvae in 6 fruits from the flies from mango and 29 in 6 fruits from those from sapote.   Six small common mangoes exposed at the same time showed 341 larvae.   It seems probable, therefore, that these large varieties from the West are less favored for attack, but that all varieties are easily infested.

Other varieties known as piña, plátano, and manzana are infested in the State of Veracruz, but a study of all these to determine the species of fruitfly characteristically attacking them has not been completed.   It is probable that at least in some cases *Anastrepha mombinpraeoptans* Seín, or species related to it, is involved, a situation which has a bearing on that in the West Indian Islands.

Prunus persica (L.) Batsch

The peach (*Prunus persica* (L.) Batsch) seems to be a favorite host of fruitflies in general, and *Anastrepha ludens* is no exception.   Bliss and McPhail [24] found the peach rather heavily infested in the region surrounding Cuernavaca, and compared reproduction in this fruit with that in pomegranate, sweet orange, sweet lime, and mango.   In

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[22] See manuscript report 57, p. 154.
[23] See manuscript report 44, p. 153.
[24] See manuscript report 8, p. 152.

Tamaulipas residents state that in the mountains where peaches are grown they contain many worms. How many of these are larvae of *A. ludens* it is impossible to say. Samples of fruit examined by McPhail contained no larvae.[25]

The reproductive period in peach, according to Stone's studies, shows about a mean of the variability in the different fruits studied. The larvae, however, break down the interior of the fruit, as can be seen in plate 2, *C*.

PSIDIUM GUAJAVA L.

The guava, called in Mexico guayaba, is widely distributed throughout that country, both wild and in cultivation. All through the central and southern parts of the country the guava is very heavily infested by *Anastrepha striata* Schiner. Very rarely *A. ludens* is reared from it. The species most commonly attacking guavas in the vicinity of Santa Engracia is not *A. striata* but another that will be discussed later (p. 138). This species appears to replace *striata* in the northern part of the Republic.

In the early days, however, guava was considered an important host of *Anastrepha ludens*, discussed at length by the workers of the Mexican Commission of Parasitology, and given as a heavily infested host by Crawford. One might be tempted to believe that guava was at one time a preferred host of *A. ludens* were it not for the comments of Rangel (*21, p. 11*) and Santillan, in Herrera et al. (*21, p. 7*), of the Commission of Parasitology. These comments make it seem fairly certain that the idea was due to misidentification.

Since the work of the Commission of Parasitology was carried out in Morelos an effort was made by Plummer in Cuernavaca to determine the degree to which *Anastrepha ludens* infests guava there. Only 2 adult females of *A. ludens* were obtained from rearings that resulted in about 10,000 adults of *A. striata*.[26] It evidently infests that fruit occasionally in nature, so the fruit may be considered as a means of carry-over. Bliss and McPhail [27] found that *A. ludens* would oviposit rather freely in guavas in cages.

It seems evident, therefore, that most of the early references to *Anastrepha ludens* in guava dealt with *A. striata* and that probably the situation then was no different from what it is now. As it is probable that all immature examples taken at quarantine, such as the 32 living puparia mentioned by Hoyt (*23, p. 310*) as being taken in guavas, have been consistently destroyed, confusion with *A. striata* would continue for lack of examination of reared adults, the method long used in the positive identification of species. That confusion of several species has been general is evident from the early Mexican plate illustrating Hoyt's article. The male figured seems to have been a male of Mexican *A. mombinpraeoptans*, the pest of *Spondias;* the female figured was probably a female of *A. ludens*, the pest of citrus and mango: and the puparia referred to were in all probability those of *A. striata*, the pest of guavas.

HOST FRUITS OF ANASTREPHA AND ARTIFICIAL INFESTATION BY A. LUDENS

A, Injury to hull of English walnut; *B*, infestation in calabaza; *C*, the true mammee apple, or zapote de Santo Domingo; *D*, the common Mexican mamey, or zapote mamey; *E*, type of package used in Morelos for shipping sapodillas or chicozapotes.
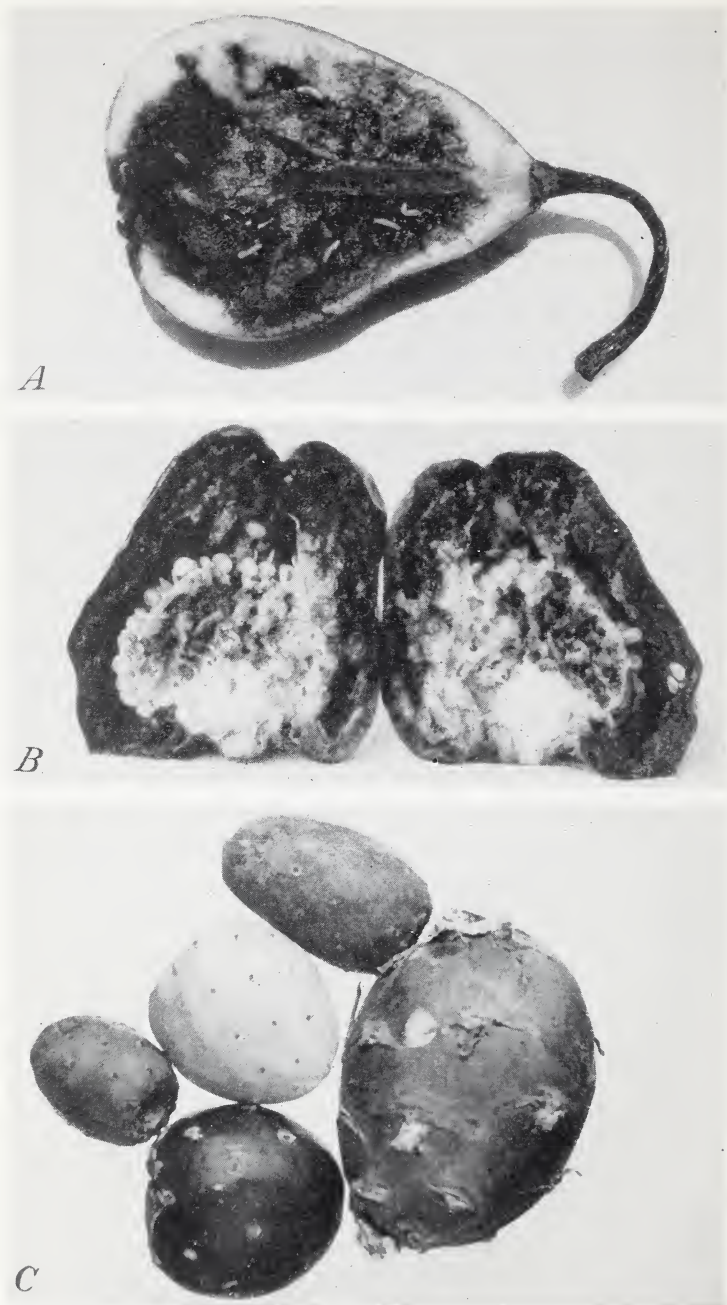
HOST FRUITS OF ANASTREPHA LUDENS

A, Pear, showing nature of infestation by maggots; B, infested bell pepper; C, cactus fruits; the smaller ones are "tunas," and the large one is a "pitaya." Cactus fruits and peppers have been infested only in the laboratory.

Punica granatum L.

The pomegranate family contains only the one species *Punica granatum* L., and the fruit is known in Mexico as granada. It is infested by *Anastrepha ludens* in nature, and was one of the fruits from which the fly was reared in Cuernavaca during the early work of the laboratory, as reported by Bliss and McPhail.[28] Skwarra,[29] working in Teotitlán, Oaxaca, found larvae in pomegranate there. In Cuernavaca it was considered of minor interest as a carry-over host, owing to the fact that it loses its fruit at much the same time as does the mango.

Pyrus sp.

The pear (*Pyrus communis* L.) is not a rule grown extensively within the present range of *Anastrepha ludens;* therefore the full possibilities of the insect in connection with that fruit are not known. Four pears containing 90 larvae, presumably those of *A. ludens*, were reported by Mackie (*25, p. 317*) on the statement of Singleton. Fruit examinations during 1931 were tabulated by McPhail,[30] and, through the kindness of T. R. Stephens and others working under the direction of Hoidale, infested pears were shown arriving on the market of Matamoros, Tamaulipas, during July, August, October, and November. Most of this fruit was from Ramos Arizpe, Coahuila.

The work of Stone has shown that pears are very abundantly infested under laboratory conditions, and it seems probable that they might be an excellent host in nature where the range of the fly is extended to include areas producing this fruit. Infestation in pear is shown in plate 6, *A*.

Apples and Quinces

The situation with apples and quinces is similar to that with pears. These fruits are not usually grown in the sections typical for *Anastrepha ludens*. At quarantine, however, fruitfly species in apples are very frequently taken. Records exist of lots of infested apples being taken at the border on 15 occasions during 1937 and infested quinces on 6 occasions. The fruits nearly all came from the Ramos Arizpe-Monterrey region. During the work in 1937 in Santa Engracia, Monk[31] obtained infested apples (perones), for sale in that region. Adults of *A. ludens* were reared from the larvae. These apples were said to have come from Galeana, Nuevo León.

In his study of duration of larval life within fruit, Stone[32] found a length of life of 30.4 days at 77° F. in apple, and this would seem to indicate that the fruit is not the most suitable for larval development. But the infestations recorded in the field in the deciduous fruits that have been mentioned show what species can do when they have continuous access to apples, pears, and quinces.

[28] See manuscript report 8, p. 152.
[29] See manuscript report 7, p. 152.
[30] See manuscript report 35, p. 153.
[31] See manuscript report 84, p. 155.
[32] See manuscript report 47, p. 153.

Sargentia greggii S. Wats.

The chapote amarillo, as it is called in northeastern Mexico (*Sargentia greggii* S. Wats.), was found infested in 1930 within the city limits of Matamoros, Tamaulipas, by inspectors on the fruitfly control work in Texas under Hoidale. It was reported also as having been found infested at quarantine on the border. The studies conducted at Santa Engracia by Plummer, McPhail, and Monk (*34, p. 6*)
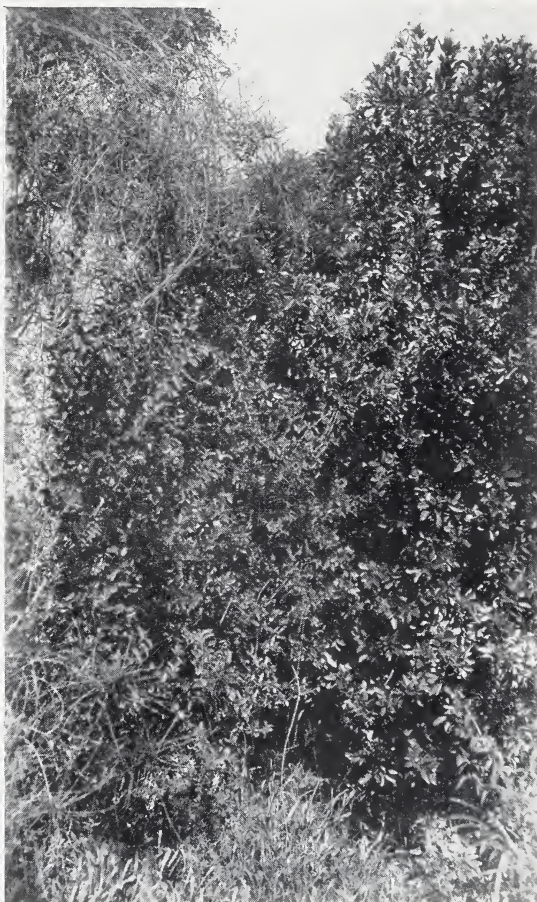
FIGURE 2.—*Sargentia greggii*, showing resemblance of large trees to citrus. (Photograph by H. S. Hensley.)

have shown this fruit to be the regular summer host of *Anastrepha ludens* in northeastern Mexico.

The tree, when growing, closely resembles certain forms of citrus on account of the appearance of the foliage. The bark is smooth and gray. Sometimes the trees are relatively large, as can be seen in figure 2, a specimen at Garza Gonzalez, Tamaulipas. The flowers are small and yellowish white and appear irregularly, since the blossoming time is rather extended. Flowers are shown in figure 3,

which was made in January as the first blossoms began to appear. The fruit is fleshy and said to be edible, is smooth, and yellow.   According to the observations of Plummer, McPhail, and Monk (*34, p. 6*),

FIGURE 3.—Blossoms of *Sargentia greggii* beginning to open.   (Baker.   *See* Plummer, McPhail, and Monk (*34*).)

FIGURE 4.—Young fruits of *Sargentia greggii*.   (After Plummer, McPhail, and Monk (*34*).)

the larvae are often found feeding in the seeds while the fruit is still rather young and the seeds are tender.   Old fruits are rarely attacked. Young fruits are illustrated in figure 4.

McPhail's records [33] indicate that *Sargentia* bloomed generally in March 1936, but in some localities green fruit was present during that month. Bloom was beginning to show a little in January 1937, when figure 4 was made. In April 1936 McPhail found 50 percent of the trees not yet in blossom, although green fruit was present in some areas. But it was from the May and June fruit that he got the heaviest emergence of flies, the greatest being in May. From 2½ quarts of May fruit 291 *Anastrepha ludens* and 324 parasites were recorded,[34] [35] and from another lot of 3 quarts 302 *A. ludens* and 79 parasites. From his later collections the percentage of recovery was increasingly less, and the last of the *Sargentia* crop dropped from the trees in the early part of August.[36]

There remains the possibility of the existence of other native hosts, and every effort is being made to discover any. These studies have been conducted mainly by McPhail, Monk, Plummer, and Shaw in Tamaulipas and by Stone in Mexico City. In the first instance, all species of wild fruits that might conceivably prove to be hosts have been collected and held for possible emergence, to determine the existence of any infestation. Work under Hoidale's direction in Texas was also conducted toward this same objective. Large quantities of wild fruits were held for emergence, but the results so far have been negative. It should be mentioned, also, that infested avocados have been found by United States border inspectors.

FRUITS INFESTED BY THE MEXICAN FRUITFLY IN THE LABORATORY

The following discussion relates to products that have not been found infested in nature but which the flies have infested in the laboratory as soon as they were given access to them. Some of these products, such as cactus fruits, peppers, and tomatoes, have been infested by the flies even when their normal field hosts were present at the same time.

Cactus

The possibility of the fruits of cactus serving as hosts for *Anastrepha ludens* has been discussed from the days of the discovery of the species in Texas in 1927, but up to the present time no field infestation has been found.

The fruits usually found on the markets in Mexico are grouped as tunas, pitayas, and pitahayas. Some idea of them is given in plate 6, *C*. Tunas are the fruits of the genus *Opuntia*, and the four smaller fruits shown are tunas. The light-colored one much resembles a peach in color and odor and is therefore called tuna duraznillo after the peach. Many kinds of tunas have been exposed to the flies by Stone, and practically all of them have been readily infested. The small sour ones called xoconostles have not been used. According to Bravo Hollis (*5, p. 142*) the most important economic ones are fruits of *O. robusta* Wendl., *O. ficus-indica* (L.) Mill., *O. cardona* Weber, *O. leucotricha* DC., and *O. joconostle* Haage and

[33] See manuscript report 65, p. 154.
[34] See manuscript report 66, p. 154.
[35] See manuscript report 67, p. 154.
[36] See manuscript report 68, p. 154.

Schmidt, although in the gardens many hybrids and varieties are grown.

The pitayas, represented by the large fruit with scales at the eyes, plate 6, *C*, belong to the genus *Hylocereus*. Stone has found that the flies deposit eggs in them immediately when they obtain access to them, and the larvae thrive in the fruit. He found the duration of life within the fruit at 77° F. to be 22 days, as compared with 20 days in peach and 25.9 days in grapefruit.

The pitahayas closely resemble the pitayas, but the scales on the surface of the fruits are replaced by groups of spines. They belong to the genus *Lemaireocereus*. These fruits also readily serve for reproduction of *Anastrepha ludens*. The pitaya shown in plate 6, *C*, was about 4.5 inches long. The pitahayas usually run a little smaller. The distinction between pitayas and pitahayas just discussed was given the senior author by Indians, but very commonly pitahaya is a general name for both.

The reason fruits of cacti are not found abundantly infested in the field appears to be the result of the habits of the adult flies. These avoid hot, open stretches where there is bright sun, and probably therefore, they do not come in contact with maturing cactus fruit. Skwarra, when working in Oaxaca, found that open cactus deserts formed a barrier against fly movement.

In the Rio Grande Valley in Texas there are cacti that bear fruits resembling the pitaya. These may be found in rather heavy, shaded cover where flies might occur, but it is very difficult to find ripe fruit, since the small wild mammals eat them before they reach that stage. Examination of large quantities of such fruit, therefore, has not been made.

Figs

Figs are very readily infested artificially, and the larvae mature in them very rapidly, Stone having found the minimum period to be 15 days at 77° F.

Bananas

Bananas are infested artificially both when ripe and when partially green. They do not seem, however, to be attractive hosts. Infestation takes place throughout the pulp, as shown in plate 2, *D*.

Walnut

One of the interesting products found to be very acceptable to the fly is the English walnut. The larvae destroy all the pulp of the husk, leaving nothing between the outer skin and the nut itself (pl. 5, *A*). In his study of the walnut husk fly (*Rhagoletis completa* Cresson) Boyce (*4, pp. 395–398*) indicates that much of the commercial loss due to that species is from shell stains which result in the nuts being classed as culls. Kernels are, however, also influenced secondarily. While no studies have been made to determine the effects on the nut itself of the destruction of the husk by the larvae of *Anastrepha ludens*, there seems no reason to believe that the injury would be less than with any other form similarly feeding.

PEPPERS

Bell peppers as well as varieties of chili peppers are heavily infested under artificial conditions. In fact, bell peppers constitute such an excellent host that Stone uses them in large quantity to obtain needed stocks of larvae. The flies oviposit in them in the presence of their normal field hosts. Stone's data show that the egg and larval stages may be passed in peppers in as short a time as 16.5 days, a period approximating that in mangoes. Plate 6, *B*, shows a bell pepper with a typical infestation. In this fruit 37 larvae were feeding throughout all parts of it.

Here again is a case of a fruit that is very readily infested when the flies are given a choice between it and their natural hosts, but in which no field infestation has been observed. The logical explanation is that *Anastrepha ludens* is a tree-inhabiting form; that it avoids open, hot, sunlit stretches devoid of shade; and that, therefore, it avoids the type of culture under which peppers are grown. This same explanation is possible in connection with other vegetable fruits to be mentioned later. Although no field infestation has been recorded, it seems well for producers to be familiar with the appearance of infested vegetables in case attempts should be made to grow peppers, etc., in an environment attractive to the flies and infestation should result.

TOMATOES

Tomatoes, like peppers, are readily infested under artificial conditions. This applies also to the small husk tomatoes grown commonly in Mexico. Stone found the duration of life in tomatoes to be as short as 20 days at 77° F. Adults emerged in 39 days.

SQUASH

The same situation occurs with the small Mexican squash, known as calabaza. Flies readily infest the vegetable, and larvae thrive in a normal manner. An infested calabaza is shown in plate 5, *B*.

BEANS

Snap beans, according to Stone's tests, may serve for oviposition and larval development, but conditions are not good for the larvae and beans appear to be unsuited as a host.

OTHER CULTIVATED FRUITS

The fly has been found by Stone to oviposit under artificial conditions in certain other cultivated fruits in Mexico. *Spondias*, loquat, and papaya become infested, as does also the fruit of *Cyphomandra betacea* (Cav.) Sendt. Of imported fruits he has found California cherry, cattley guava, Natal plum, and Spanish plum to be infested artificially. *Feijoa sellowiana* Berg proved to be one of the most abundantly and easily infested fruits tested.

WILD FRUITS

Very few wild fruits have been infested artificially. Of the various ones tested exclusive of *Sargentia* and varieties of *Cactus*, only *Bumelia laetevirens* Hemsl. has served for satisfactory reproduction.

This fruit, which is called tempixtle (*30*), is a relative of the coma (*B. spiniflora* A. DC.) found along the border, the berries of which serve as a host of another fruitfly (*Pseudodacus pallens* (Coq.)). Tempixtle was found by Stone to be a rather satisfactory host for *Anastrepha ludens* under artificial conditions, the life within the fruit being as short as 19 days and adults appearing in 35 days.   This fruit apparently does not occur along the Rio Grande, but only southward. It has not as yet been studied by the authors in nature.   Coma berries remained uninfested when exposed to *A. ludens.*

A large fruit from Cuernavaca called pancolote by the Indians there was exposed by Stone,[37] who found that larvae of *Anastrepha ludens* developed in it but pupated in the fruit.   A malformed adult was found in the interior.

FRUITS UNSATISFACTORY AS HOSTS

In a number of fruits to which flies were given access in the usual way in the laboratory no infestation occurred; or larvae, if produced, failed to survive.   These included the lemons and sour limes, lima beans, cantaloup and honeydew melons, chayote, okra, cucumber, and chilacayote, a melonlike fruit.

HOST PREFERENCE

Host preference is a question not easily decided.   It involves suitability of larval food, preference of adults for oviposition. environment sought by the adults in general, including the suitability of the environment produced by different growing trees, and, finally, the question of the food of the adults apart from the general influence of environmental factors.

Crawford (*7, p. 461*) indicated that flies had not been observed to oviposit in fruits other than those he listed.   These included ciruela (*Spondias mombin* L. (*purpurea* L.)) and guava, but it is not clear that he made oviposition observations on these fruits.   In the earliest studies in Mexico, Rangel, in Herrera et al. (*21, p. 12*), made choice tests with orange and guava.   One fly oviposited in guava once; the others chose orange with repeated oviposition.

In applying the usual criterion for determining preference for oviposition, Santillan, in Herrera et al. (*21, p. 10*), mentioned that 6 to 24 larvae were usually found in mangoes and oranges.   The number varies considerably, Stone having recorded as high as 117 larvae from a single mango from Cuernavaca.   Crawford (*7, p. 461*) indicated that grapefruit is preferred in the Tampico area, sweet oranges not being attacked until the grapefruit season is past.   Skwarra [38] lists grapefruit as the most favored host in Mata de Zopilotes, but not in Oaxaca or Morelos.   Baker [39] found grapefruit the most heavily infested at Santa Engracia.   Of 132 fruits examined, 108 contained visible larvae.   In a short time 9,000 grapefruit were buried as they fell.   Of 525 navel and Parson Brown oranges examined at the same time, 98 contained larvae, while of 395 half-bloods 47 contained larvae. The grapefruit had all dropped by the middle of November, and at

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[37] See manuscript report 51, p. 153.
[38] See manuscript report 24, p. 153.
[39] See manuscript report 61, p. 154.

that time the grove manager estimated a 25-percent loss in the navels. Sour oranges were less heavily infested.

McPhail and Bliss (*29, pp. 6, 7*) conducted experiments on the choice made by the fly both for oviposition and feeding. Green and ripe mangoes and guavas were used. For oviposition mango was decidedly preferred over guava and, incidentally, the selection of green fruit over ripe fruit was shown. For feeding, mango was also preferred over guava and ripe fruit much more than green fruit.

The selection of fruit by adults for feeding is far less specific than their choice for oviposition. This would be expected. McPhail and Bliss (*29, pp. 6, 7*) made studies on food selection, using pieces of cut fruits and whole fruits, and checking sugar solution against the cut fruits. The fruits exposed were mango, orange, and guava. They found that there was a decided preference for mango, both whole or cut, the preference being greater for whole mangoes.

Santillan, in Herrera et al. (*21, p. 12*), anticipating the use of sweetened poison as a spray, found that adults enjoy sugar solutions and especially the exuding liquids from the skins of orange, apple, and guava.

Skwarra [40] made extensive observations on possible food supply in the field. She never found the flies feeding on lima, or sweet lime fruits. In her experience the honeydew of aphids appeared rather repellent than otherwise. Blossoms of many kinds were investigated, including those of orange and mango, but she did not find any feeding there and concluded that the flies do not seek blossoms. She did not observe them feeding on sugarcane, although she did find them in numbers on the leaves of corn plants in Teotitlán, Oaxaca, and concluded that this was a definite source of food, at least in that locality.

Baker, in 1927 and 1928, found the flies feeding on fallen mangoes under the trees in Cuernavaca. The habit has been repeatedly observed in subsequent years. It seems probable that the environment in which the fallen fruit happens to be may play a considerable part in selection by the fly.

Darby and Kapp [41] reported that *Anastrepha ludens* feeds on yeasts and in publication (*14, p. 9*) asserted that "*Anastrepha ludens* in its normal habitat feeds largely if not exclusively on yeasts." If this is the case it is important in the development of methods of control.

Their evidence is as follows, quoted from their report:

An artificial medium (see Appendix I), was made with the single source of food, the yeast, carried to it on the legs of the fly itself. On this medium the flies have lived for two and a half months.

The formula given by them in the appendix is as follows:

Knop solution	250 cc.	Distilled water	750 cc.
Cane sugar	100 gs.	Corn meal	125 gs.
Agar	15 gs.		

Their assumption that this medium contained no other source of food than the yeast accidently carried on the legs of the flies appears scarcely valid in view of the amount of sugar present.

Several observations by others have not so far confirmed the opinion of Darby and Kapp. Mooser and Baker were unable to demonstrate

yeasts in the alimentary tracts of young adults, either from smears or from serial sections of entire flies, although bacteria were abundantly present in certain portions of the gut. J. Stern, of the Mexican Instituto Biotécnico, a specialist on yeasts, confirmed the absence of such organisms in the preparations.

McPhail has repeatedly shown that flies desert mango trees after the fruit drops, and Baker was able to culture yeasts from the foliage so deserted. On the other hand, D. F. Starr was unable to demonstrate sugars on the surfaces of young mango leaves.

Baker tested equal populations of adult flies, the one receiving sugar and distilled water and the other yeast and distilled water. The population on yeast died rapidly much as in starvation, all being dead by the end of the fourth day. The mortality on sugar was no greater than that with stock populations.

Since no trouble has been experienced in rearing *Anastrepha ludens* in the laboratory without yeast, as distinct from difficulties encountered with *Rhagoletis pomonella* (*19*)—difficulties overcome by including yeast in the diet (*17, p. 78*)—an added evidence is given to indicate that yeast is not the usual food of the Mexican fruitfly.

In 1931 Plummer undertook feeding tests with numerous chemically pure carbohydrates, distilled water being provided in containers for the flies to drink. Not all the tests were completed, since in some cases flies were still alive when more important studies forced the closing of the experiments. Where flies survived for long periods the populations died in a gradual manner. Control flies which had access only to distilled water lived 5 days. Durations of life on the different materials are given in the following list, in which the tests that were run until all the flies had died are indicated by asterisks.

Material:	Maximum duration of life in days	Material:	Maximum duration of life in days
Dextrose	*176	Trehalose	64
Levulose	*194	Melezitose	*176
Galactose	127	Raffinose	*152
Mannose	*52	Dextrin	*144
Maltose	*166	Starch	*5
Sucrose	194	Rhamnose	*4
Lactose	*5	Xylose	*4
Cellose	*7	l-Arabinose	*7
		Melibiose	*18

From these figures it is evident that with lactose, cellose, starch, rhamnose, xylose, and *l*-arabinose death was of the same order as that of starvation. The results with melibiose are noteworthy, since two-thirds of the flies died during the first 6 days. With trehalose two-thirds of the flies were still alive at the end of 64 days, when the experiment was discontinued. The results with raffinose are interesting, since honeybees, according to the work of Phillips (*31*), were unable to utilize it; and the same is true of galactose, on which there was a good survival. Since the flies used in all tests were from 21 to 27 days old at the beginning of the experiments, the survival of 5 or more months obviously shows a satisfactory utilization in many cases.

Studies with *d*-mannitol, erythritol, and amygdalin gave very low survival time—15, 3, and 11 days, respectively. A survival of 15 days

in the first case and 11 days in the third case may represent some utilization.

In 1935 Plummer tested a sample of d-mannoketoheptose, received from the Bureau of Chemistry and Soils, on which the flies lived 8 days.

Considering all the preceding observations and the little that is yet known regarding the metabolic functions of *Anastrepha ludens*, it appears wisest to reserve opinion on the idea that flies feed "largely if not exclusively" on yeast, as expressed by Darby and Kapp, and to continue using sugar as the food element in poison sprays when one is necessary.

The question, however, as to whether flies prefer to congregate in grapefruit trees, in sour orange trees, or in various varieties of sweet orange can be determined only by a study of the populations occurring in such trees throughout a season. McPhail undertook such a study, reporting final details up to September.[42] McPhail's data shown in table 1 represent the average catch of 25 traps counted at intervals through each half month. They show the same type of fluctuation in all citrus. Spraying experiments were begun in some of the groves in the fall, and this naturally upset existing populations.

TABLE 1.—*Seasonal distribution of adults of Anastrepha ludens in citrus trees of different varieties as indicated by the average catch in 25 traps*

Period	Grape-fruit	Navel orange	Valencia orange	Sour orange	Period	Grape-fruit	Navel orange	Valencia orange	Sour orange
1936	*Number*	*Number*	*Number*	*Number*	1936	*Number*	*Number*	*Number*	*Number*
Jan 1–15	143.9	176.6	189.3	----------	June 1–15	5.0	5.2	6.1	4.5
16–31	140.3	148.7	62.4	----------	16–30	1.3	3.5	.8	4.1
Feb. 1–15	48.7	----------	28.9	22.4	July 1–15	.9	1.1	.7	3.0
16–29	67.2	38.0	30.4	30.3	16–31	0	2.5	.7	2.1
Mar. 1–15	53.6	28.8	34.7	34.6	Aug. 1–15	.2	3.1	.3	1.0
16–31	138.8	72.3	77.8	25.2	16–31	.8	2.1	.2	.3
Apr. 1–15	51.3	5.2	41.3	15.2	Sept. 1–15	18.2	54.4	1.7	13.3
16–30	4.8	2.2	5.4	3.0	16–30	43.4	53.7	6.2	----------
May 1–15	14.7	2.0	4.3	8.0					
16–31	12.3	3.1	13.0	4.8					

As has previously been indicated, heavy infestation may be a reflection of factors other than fruit preference. The sour oranges at Santa Engracia are planted in a long, open row along the road to the hacienda compound (fig. 5, *A*). At Hacienda El Roble, a few miles away, however, sour oranges are planted in grove formation, and the senior author found them heavily infested and the ground beneath the trees thickly covered by fallen fruits. On the other hand, at a nearby hacienda grapefruit are planted along a mule road much as the sour oranges are at Santa Engracia, and the trees are of about the same size. Baker found this grapefruit heavily infested, while the infestation in the sour oranges at Santa Engracia at the same time was relatively light. Factors other than fruit preference enter in such cases.

The apparent preference shown by the flies for different fruits for oviposition prompted Crawford (*7, p. 193*) to recommend the planting of grapefruit among oranges with the idea that the flies would choose

Figure 5.—Citrus plantings at Hacienda Santa Engracia, Mexico: *A*, Arrangement of sour orange trees along the road; *B*, old navel orange grove showing shaded condition.

the grapefruit and that thereby the oranges would be protected. Skwarra [43] after having observed heavy infestation in sour oranges in southern Mexico and probably influenced by Crawford's statement, proposed the same kind of a plan for the use of sour orange.

In Santa Engracia, as just mentioned, sour oranges are planted in a row along the roadside and just beyond the fence is a block of oranges, part of which can be seen in figure 5, A. This, to some degree, fulfills Skwarra's ideas of sour oranges planted with sweet ones to protect the latter. Actually, however, no such protection took place, and the sour oranges were themselves lightly infested.

Grapefruit occurs in Santa Engracia along with numerous varieties of oranges; yet the grapefruit has not protected the oranges. Flies entered both in the fall, and both became infested. The earlier the fruit, the heavier the infestation. It seems evident, therefore, that planting susceptible varieties to protect others would be undesirable.

It is common observation that *Anastrepha ludens* seeks shade. Certain types of foliage are therefore more attractive to it than others. Old shaded groves are more likely to be infested. In Santa Engracia infestation has been heavier in the old navel grove than in any other orange block. Figure 5, B, shows the close, shaded character of this grove. It is cool and moist. The permanent irrigation canal runs along the side of it. Next in density among the oranges is the end block in the half-bloods. The shaded effect can be seen in figure 6, A. On the other hand, the Parson Browns are younger trees and more open, each standing much by itself, as seen in figure 6, B. The Valencias are very similar. It is obvious, therefore, that these groves are very different and, other things being equal, the largest population would be expected in the navel grove and, as a result, the heaviest infestation.

The unusual infestation of 1936–37 in Texas has thrown considerable light on infestation by the fly in large grapefruit areas. The fact that old shaded groves (fig. 7, A, B, C) offer an environment most suitable to the fly cannot, however, be accepted as indicating that infestation may not occur in other environments. Practically all types of citrus trees evidently harbored flies, for citrus in all environments became infested. Small trees in open rows (fig. 7, D) somewhat comparable to the Parson Brown in Santa Engracia showed infested fruits. A very small grapefruit tree in an open area (fig. 8, A) bore in all 48 fruits, of which 24 proved to be infested.[44]

The heavy infestations in the Santa Engracia area are no doubt somewhat influenced by the general environment there, outside of fruit preference itself. The location is that of a river valley. In the background are the mountains, and not only the Santa Engracia River takes its course through the hacienda, but several small streams as well. A large artificial lake serves for continued irrigation. The valley as a whole is sometimes subject to mists, and the leaves of the citrus trees quite commonly drip in the morning from dew. While territory surrounding the hacienda shows cactus growth and other evidences of an arid environment, nevertheless the situation is rather marked along the river itself by the Spanish moss and other growths visible, an environment typically illustrated in figure 8, C, taken on the river not a great way from the hacienda compound.

[43] See manuscript report, 24, p. 153.
[44] See manuscript report 73, p. 154.

One point of difference, however, should be noted. In Texas the trees are headed low, so that even with relatively young trees the aprons touch the ground. This is not the case with some of the young

FIGURE 6.—Citrus planting at Hacienda Santa Engracia, Mexico: *A*, Half-blood orange grove showing shaded condition; *B*, Parson Brown grove showing open nature of planting and high-headed trees.

groves in Santa Engracia, as may be seen by comparing figures 6, *B*, and 7, *D*. The low-headed trees offer ample shade for the flies in the tree interiors. Figure 7, *A*, shows the appearance of the rows after
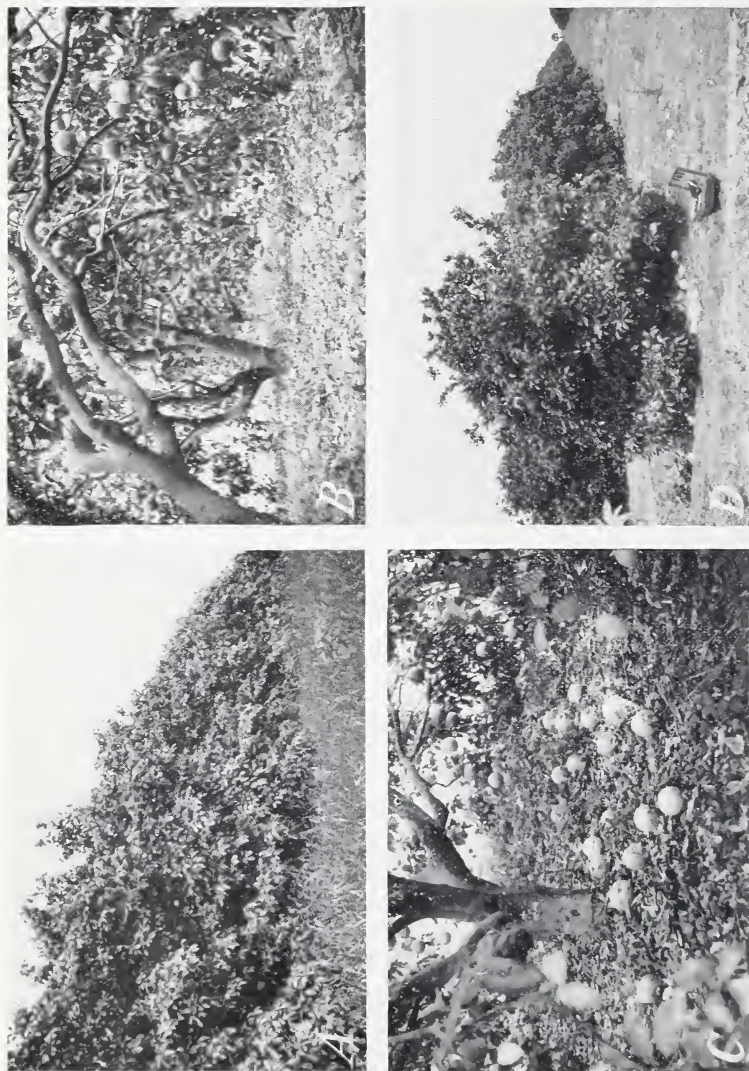
FIGURE 7.—Shaded conditions favorable for the Mexican fruitfly: A, Old tree rows in Texas, showing close, shaded nature of growth; B, interior of the rows shown in A showing the fruit borne in the interior of the trees; C, infested fruit under old trees the aprons of which touch the ground; D, young trees in Texas, showing trees headed low and with shaded interiors.

FIGURE 8.—Various environments where host plants of the Mexican fruitfly have been found infested: A, Hot, open site in the Rio Grande Valley with a small grapefruit tree that was heavily infested during the season of 1933-37; B, scene at Chapul with citrus tree in center; C, along the river at Santa Engracia, showing Spanish moss and other evidences of humid conditions; D, wild environment south of Chapul in which Mexican fruitflies were taken in traps.

the trees have become well developed. The fruit is largely borne in the shaded interiors, as may be seen from figure 7, *B*, a photograph taken inside the drooping apron. Fruit infestation was evident under such conditions as is shown in figure 7, *C*. Another factor which has, probably, some significance is the occurrence in some places of heavy windbreaks furnishing a shelter for the flies. Infestation was notably heavy near these windbreaks.

It does not follow, however, that environments such as those described, while favorable, are necessary for the fly, a fact which is evident from the trap catches made under the direction of Hoidale in the wild land south of Reynosa. Flies were caught throughout this land extending a long way south of the border. Small villages are found rather widely separated throughout this territory, and it is true that in these villages there are occasional citrus trees. Figure 8, *B*, shows the growth at the small village of Chapul, which, with its citrus tree, is typical. However, 10.3 miles south of Chapul flies were taken in the midst of a purely wild territory, the environment of the exact spot being shown in figure 8, *D*. It is evident that these widely scattered villages with their very few citrus trees are of insignificant influence in the whole area occupied by the fly. The region has considerable cover, as can be seen from figure 8, *D*, and it is not therefore an open territory in the sense of some of the cactus environments. Along the water courses especially the tree growth is of considerable extent. It is along the rivers or ravines that *Sargentia* grows most abundantly.

HOST SEQUENCE

Host sequence presents several problems owing to the fact that some hosts, either wild or cultivated, are more common or more important in some areas than in others. Usually one host is dominant. These appear to be (1) the common mango, (2) citrus, and (3) *Sargentia*. In addition to these there is another sequence in which no dominant host is apparent.

The sequence dominated by the common mango has been studied extensively in Cuernavaca where only a small amount of citrus is grown. De la Barreda, in Herrera et al. (*21, pp. 34, 117, 118*), listed mango as the principal source of *Anastrepha ludens* and included sweet lime as the main winter host. McPhail and Molino[45] reported recoveries from orange, peach, guava, and ciruela (*Spondias* sp.) during the off-mango season but gave no opinion as to the species involved. Bliss and McPhail[46] definitely eliminated the guava and ciruela species and added pomegranate in the sequence of fruits infested.

McPhail[47] followed the fruiting sequence of various trees and concluded that in Cuernavaca, by reason of the scarcity of oranges and peaches and the fact that pomegranates disappear along with mangoes, sweet limes serve as the best carry-over among the minor hosts. They are not an important factor, however, in continuing the infestation in Cuernavaca.

[45] See manuscript report 6, p. 152.
[46] See manuscript report 8, p. 152.
[47] See manuscript reports 14, 16, p. 152.

Skwarra [48] emphasized the part played in the sequence by the mango, which she found blossoming irregularly everywhere, sometimes only on one side of a tree at a time. She recorded the sequence as including mango (in October), early and late oranges, tangerines, and green mandarins. Sour oranges she recorded as present throughout the year and pointed out that the different varieties of citrus give a complete yearly sequence for the fly.

Stone and Plummer,[49] and later Stone especially, carried on extensive observations on the fruiting of mangoes, using at first 330 trees and later 356, and giving monthly records of trees in bloom and trees
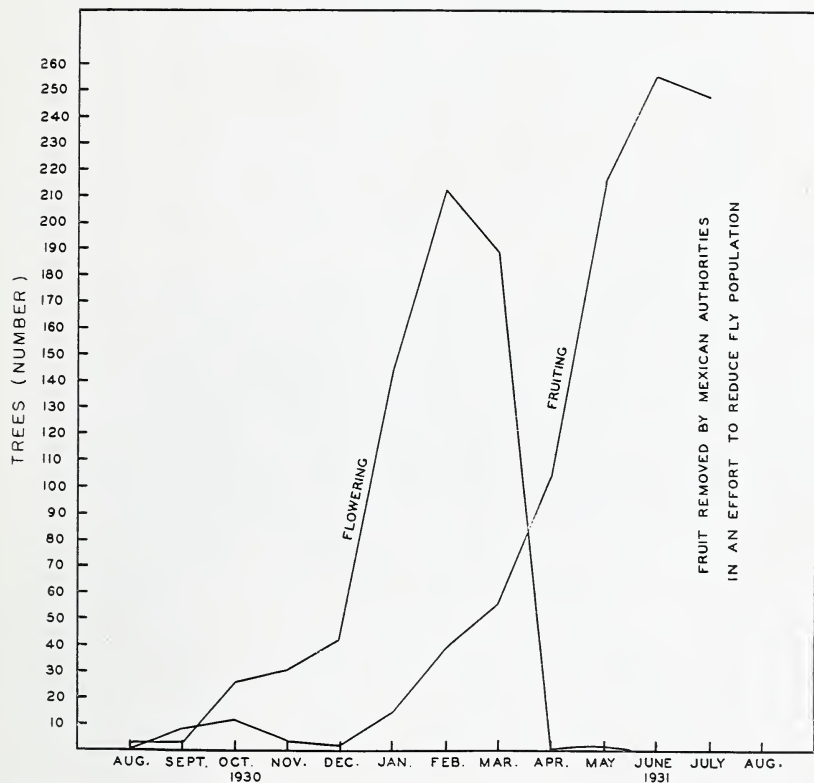
FIGURE 9.—Annual course of flowering and fruiting of mango trees in Cuernavaca, Mexico.

dropping fruit. Figure 9 shows the relation found. It will be seen that mangoes offer almost a continuous availability in Cuernavaca, which undoubtedly accounts in part for the heavy population there. The records in this case were not completed for the yearly cycle, because the Mexican authorities removed the fruit from the trees at the end of July in an effort to reduce fly population.

Later, in 1933, the Mexican Government attempted to control the fly by cutting back all mango trees in Cuernavaca in order to pre-

[48] See manuscript report 24, p. 153.
[49] See manuscript report 28, p. 153.

vent their fruiting, hoping in this way to starve out the flies. Unfortunately this effort was unsuccessful, since a sufficient number of flies carried over and reproduced in other fruits or stray mangoes to reinfest the mango crop when the trees came again into bearing.

In Cuernavaca, McPhail [50] followed the occurrence of adults throughout the year in mango trees, especially guavas. He found definite migrations from mango trees, after the fruit had fallen, to guava bushes in fruit, although the females seldom utilize guavas for oviposition (fig. 10). It is instructive to compare this figure with figure 9 showing the fluctuation in the blossoming of mango trees in the same region and the availability of mango fruit.

Darby and Kapp [51] studied the influence on infestation of the fruit sequence of an individual mango tree. The number of larvae per fruit gradually rose from 13.2 on December 5 to 56.9 on February 23.

Domination of a sequence of hosts by mango also occurs in places where citrus is grown more extensively than in Cuernavaca. This is shown in the studies by Baker [52] in the region about Tequila, Jalisco. Mango plantings are heavily infested. In citrus groves the population of flies is high by reason of the earlier infestation in mangoes. Glass traps placed in citrus trees for a single day captured from 12 to 25 flies per trap.

Domination of a sequence of hosts by citrus, probably grapefruit, is shown by the studies of Crawford (*7*, *pp. 461, 462*) in the vicinity of Tampico, Tamaulipas. He stated that mangoes there are almost never infested. The only sequence he considered necessary is the sequence of citrus fruit in the grove, i. e., from grapefruit to later orange, to off-bloom grapefruit, to the fruit of the maturing crop. Crawford (*8*, *pp. 180, 181*) listed four periods of adult population. The first was in February and March, the flies having emerged from the infested crop of January and February; the second, much reduced in number, was in June and early in July; the third, showing very small numbers, was in September and October; and the last was in December, from the October oviposition. Thus he attributed the heavy infestation in the main crop to a second generation from it. The data and arguments presented by Crawford have had a distinct influence on subsequent conceptions regarding grove sanitation.

The third sequence, in which there is dominance by *Sargentia*, had its inception when McPhail, [53] through the courtesy of Hoidale, studied the work of the control forces in Matamoros. McPhail emphasized the discovery there in 1930 of infestation in *Sargentia greggii*, there being 54 trees of this species scattered throughout the city, and the infestation taking place in the summer.

When work was begun in Santa Engracia and traps became available, McPhail [54] undertook a study of the wild land, especially the extensive growth of chapote amarillo, as *Sargentia* is called around the hacienda, basing this effort on the earlier discovery at Matamoros. Later, during summer, he reared large numbers of flies from the *Sargentia* fruit. The continued study of the populations in *Sargentia* throughout the season has accumulated data indicating

[50] See manuscript report 82, p. 154.
[51] See manuscript report 15, p. 152.
[52] See manuscript report 50, p. 153.
[53] See manuscript report 25, p. 153.
[54] See manuscript report 64, p. 154.
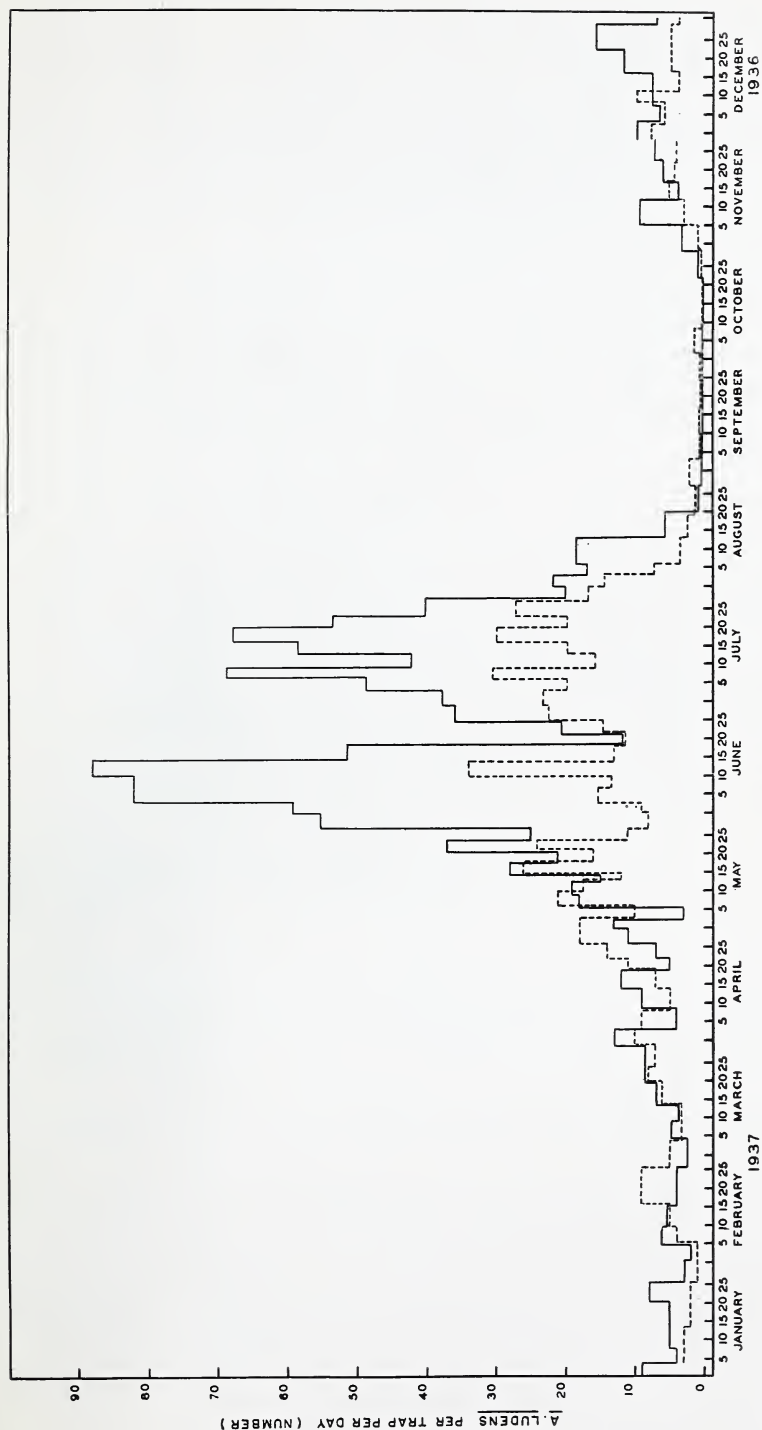
FIGURE 10.—Annual sequence of adult populations of *Anastrepha ludens* in mango and other trees in Cuernavaca, Mexico. Solid line represents mango population and the broken line, population in miscellaneous trees.

clearly the role this fruit plays in relation to citrus production in the northeastern part of the Republic.

Figure 11 plots the population in grapefruit and in *Sargentia* largely from McPhail's seasonal data obtained in 1936. The first striking thing is that the early winter infestations in citrus are due to a heavy incoming population in the fall. This population apparently results when the large summer population in *Sargentia* begins to move and, finding citrus groves, moves into them as well as elsewhere. It is not necessary to postulate a build-up from the small summer population in the grove.

There is, of course, a difference between seasons. In 1936 the population fell away during November and December. But in 1935 the population was so high during November that it remained high during December and January, gradually falling away in February and early March. This accounts for the high peak in January 1936. The March peak in citrus is obviously due to oviposition by the
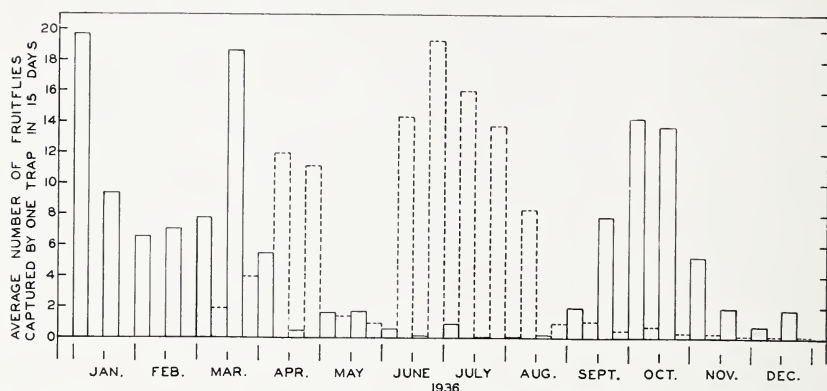
FIGURE 11.—Annual cycle of abundance of *Anastrepha ludens* in grapefruit and *Sargentia* at Santa Engracia, Mexico, 1936. Solid line represents captures in grapefruit and broken line captures in *Sargentia*. (After Plummer, McPhail, and Monk (*34*).)

fall and early winter flies and the resulting adults which emerge during this time.

In the meantime in *Sargentia* there were two peaks, one in the spring and one, a heavy population, in summer. The occurrence of two peaks rather than one may be variously interpreted. Only one season's trapping results in *Sargentia* are available, and it is possible that the results of other seasons would differ from those of 1936. Several things, however, seem obvious, among them that the flies leave citrus, and that the summer generations produced in *Sargentia* spread out and, if they encounter citrus groves in the fall, infestation results.

It will be seen that the April peak in *Sargentia* is followed by a large summer population. This may or may not be the case each year. There are no records to show why the April flies left *Sargentia* or where they went. Nor are there data to show why the flies leave the citrus groves in April or why they leave them again in November or later. Presumably they possess some definite migratory instinct. One thing, however, appears evident, namely, that *Sargentia* is the

important factor. The population in *Sargentia* is presumably the original one and, as this begins to move, citrus, incidentally in its path, services as a convenient location for congregation and extensive reproduction.

The data presented in figure 11 appear to have a bearing on the occurrence of *Anastrepha ludens* in the Rio Grande Valley of Texas. Large populations appear in the Valley in the early winter, considerably later than they appear in Santa Engracia.[55] During the summer months few, if any, flies are taken in the Valley. A few occur
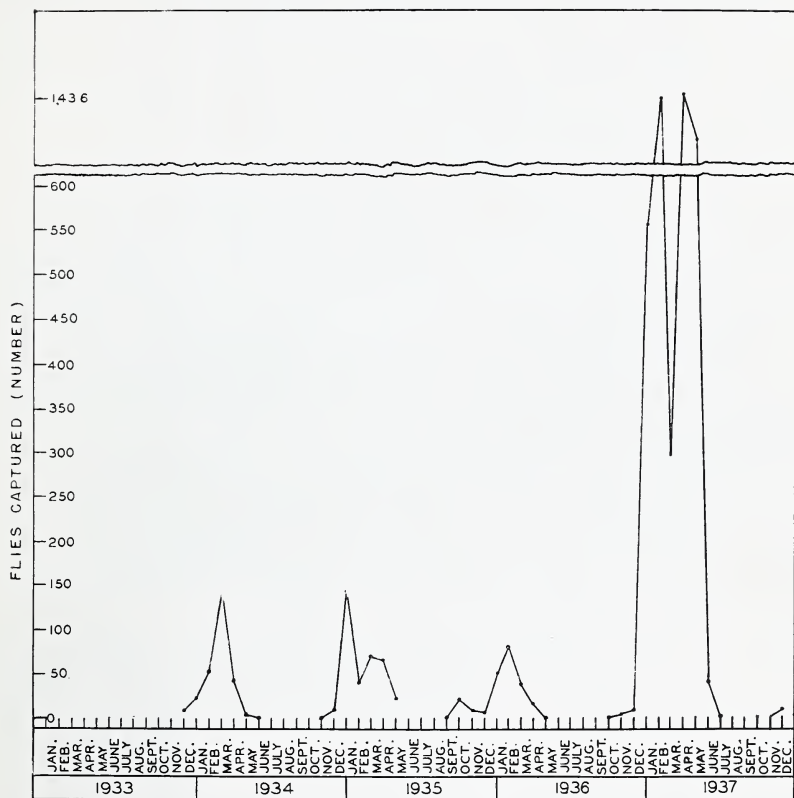
FIGURE 12.—Annual occurrence of adults of *Anastrepha ludens* in the lower Rio Grande Valley, Tex. (Data from reports of M. H. Ford and N. O. Berry.)

in groves in Santa Engracia, even after the population as a whole has left. Figure 12 shows the captured populations in the Valley during four seasons. The season of 1933–34 was unusual by reason of the storm, and the curves in any case are not entirely comparable on a trap basis, although they will serve for illustration.

There are no data for 1934–35 for Santa Engracia, as work had not been begun there, but the season in the Rio Grande Valley may be

[55] Data from the various reports prepared under the direction of P. A. Hoidale.

considered typical. One fly was trapped in November. During December, 10 flies were taken. Then during January the bulk of the population appeared. And it is noteworthy that, following this rise in the groves, fruit infestation was discovered in February. It will be noted that a secondary peak occurred in March and April. There is no escaping the conclusion that this peak was due to flies emerging in the Valley from oviposition during the time of the major peak. But these resulting flies left the groves in the spring.

Compared with the 1934–35 curve it will be seen that in 1933–34 the major population was 2 months later, having its peak in March. And it is worthy of note that the first fruit infestation was found in April, also 2 months later. From this infestation, however, there was no secondary build-up of adults, since it could not, under Valley practice, have been generalized sufficiently in the main crop to be reflected in the captured population: moreover, flies emerging would presumably begin their spring movement.

In Santa Engracia in 1935–36 the influx from the wild land took place early. In the middle of October the grapefruit was heavily infested and dropping badly. Before November had passed, the crop had all been destroyed. In the Rio Grande Valley also the flies appeared very early, one fly being taken in September and a considerable peak occurring in October; fruit infestation was found in December, months earlier than in the 1933–34 season. The early appearance in the Rio Grande Valley had its reflection in early infestation as it did in Santa Engracia, and presumably the resulting peak in February, which represented the main population, received a contribution from flies emerging in the Valley.

The season of 1936–37 was remarkable for the very high population occurring and the heavy infestation resulting. As will be seen from figure 12, there was a very high secondary peak, the result of the emergence of a large population in the groves in the spring. This population peak occurred in April, but the flies rapidly disappeared from the groves.

Several things, which at present cannot be explained, are evident from this figure. Following the heavy population in Texas the flies leave the groves. It may be assumed that this is because the fruit has been harvested. But in Santa Engracia flies leave even while fruit remains. It is possible that there is a heavy death rate, but, as will be seen from the longevity studies, if flies are kept in captivity they continue to live. The host-free period in the Rio Grande Valley, eliminating any secondary host like *Sargentia*, may make the whole area unattractive to them. All that can be said with certainty is that the flies appear in large numbers, that again they disappear, and, judging from experience in Santa Engracia, that they scatter.

The picture as developed to date, however, is instructive on one point. Before it was visible, ideas were based on the story as developed by Crawford and on observations which tended to confirm that story as applicable to all citrus properties. Trapping procedure as an index had not then been developed. In the light of the knowledge at that time, therefore, the period in which to apply sprays to eradicate or control the pest was when it was weakest, during the low populations described in the summer. This had proved effi-

cacious with the Mediterranean fruitfly (*Ceratitis capitata* (Wied.)) in Florida. In a period extending from near the end of July to early in August 1932 all bearing citrus trees in the lower Rio Grande Valley were given one application of nicotine sulfate and molasses spray. The majority of the trees were sprayed a second time with the same compounds between early August and the middle of September. The anticipated results did not follow and extensive spraying was discontinued. Negative trap results following the campaign were only misleading.

It seems evident now from data from all sources that it is quite beyond human possibility to eliminate the fly during the off-season, since populations are widely spread throughout its native habitat. Recourse can be had only to protection timed to destroy flies when they appear in the groves. From the comparison of the curves in Santa Engracia and in the Rio Grande Valley, this timing would necessarily be different for different localities. Experimental effort to apply this idea is recorded under the discussion of toxicity and spraying.

Aside from the special sequence that has been discussed between the native summer host of *Anastrepha ludens* and citrus, there is, of course, the sequence mentioned by Crawford between the different varieties of citrus in the groves themselves. It seems hardly necessary in this connection to discuss the early, midseason, and late varieties of citrus. But it is worth mentioning that the grapefruit in Santa Engracia is the earliest citrus to mature. It therefore becomes the first and most heavily infested. The early navel oranges mature next, and these are next to the grapefruit in their degree of infestation. The flies moving in the fall apparently blanket groves of all types, but they remain and build up their numbers in those having the earliest maturing fruit, although they may leave the late Valencias for the wild land in the spring while these trees are still full of fruit. This is the condition of typical citrus properties where there are groves each representing a different variety and where *Sargentia* is in the vicinity.

The category in which no dominant host is apparent is shown in some of the more tropical parts of Mexico where there are commonly large numbers of dooryard gardens, each planted with miscellaneous fruit trees. For example, in Teotitlán, Oaxaca, Skwarra [56] found one garden with fruit trees of 11 different kinds, and in another garden she reports 9 kinds of fruit trees. In this general region there is usually one main mango crop, or, according to Skwarra, occasionally two, but citrus is available during the entire year. In her work during November alone she found the following infested by *Anastrepha ludens:* Grapefruit, sweet orange, mandarin orange, sour orange, sweet lime, pomegranate, and mango. It is not surprising, therefore, that infestation would be heavy with this sequence available, a fact illustrated by an examination of 20 sweet limes under one tree, only 3 of which showed no sign of infestation.

Host-Free Period

A host-free period is a period during which no fruit known to be infested in nature by a species is allowed to reach the stage susceptible to attack. The host-free period is sometimes erroneously confused

[55] See manuscript report 7, p. 132.

with a period of a length that will result in the complete elimination of a pest. This usually requires a period of years and is in reality a noncrop period.

In the correct sense, the purpose of maintaining a host-free period is to prevent the building up of populations of a pest during the off-season of its commercial hosts. Under these conditions it cannot be hoped to eliminate the pest, but absence of fruit can prevent its increase to numbers that would jeopardize the crop when it comes into production.

When *Anastrepha ludens* was discovered in the Rio Grande Valley of Texas in 1927, one of the regulations established (*45*) provided for the promulgation of a host-free period beginning in March and continuing for 7 months. Before the commencement of this period it was required that all commercial citrus be removed from the trees and that all other hosts be destroyed, either by removal of the fruit or elimination of the trees. Such a regulation gave no opportunity during the summer months for reproduction of the flies in the area involved.

The subsequent history appears to have confirmed the wisdom of this regulation in regard to secondary host fruits. In areas farther south flies leave the citrus groves, move a short distance to areas occupied by *Sargentia*, and there build up large populations during the summer. These alternate host fruits are sometimes scattered about on the haciendas between or near grove plantings, and they furnish a recurrent source of flies close at hand.

In the Valley it has been impossible to recover flies in any numbers in traps during the summer season. Instead of remaining as in Mexico to build up populations in secondary fruits they apparently leave the Valley. Just what happens to them has not been determined, but a new generation does not emerge in summer fruits in the Valley to be present there in numbers to attack the first ripening citrus. It is true that flies appear, often as large populations, in the early winter, but whatever the origin of these flies they are not augmented by a large continuing summer population.

STUDIES ON THE LARVAE

Appearance of the Larvae

The larvae, when found within the fruit or when just emerged from it before entering the ground, may be seen as white, grublike forms, pointed at one end, where the black mouth hooks are visible. The general appearance is shown in figure 13, *A*. Occasionally larvae may be attacked by disease, or may die within the fruit from other causes, and under these circumstances they usually become dark brown or black. A diseased larva appears in the illustration.

The posterior breathing slits are located at the larger end of the larva (fig. 13, *B*). These structures and others permit identification, but it is difficult to distinguish larvae of closely related species. There often occur in fruit other larvae which in general very closely resemble those of fruitflies and are often mistaken for them. Such larvae do not destroy sound fruit but attack it only when it has been previously injured or decayed. They are not of economic importance. Such

inoffensive larvae usually possess quite a different type of breathing slit. Two black knobs protrude from the larger end of the body of most of them, so that such larvae can be easily distinguished from those of fruitflies.

A spiracular plate of the larva of *Anastrepha ludens* is shown in figure 14, *A*. The specimen figured was prepared in January 1933. As a check against it figure 14, *B*, shows the first spiracle of a preparation of 1932 from mango; figure 14, *C*, one from a 1937 preparation from sweet pepper; and figure 14, *D*, is one from citrus in 1937 made from a specimen from Santa Engracia. Each preparation is from a larva picked at random. This accounts for the curved condition of the spiracle from pepper. Another larva from pepper would in all probability have had a straight spiracle.
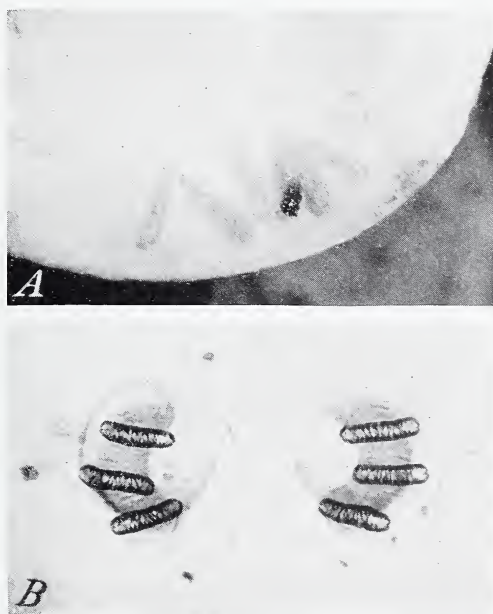
FIGURE 13.—Larvae of *Anastrepha ludens* from infested grapefruit: *A*, Larvae, slightly more than natural size; *B*, posterior spiracles, greatly magnified.

An illustration of the larva is shown in figure 15. The larva possesses no legs, but progresses by means of expansion and contraction of the body segments. Swellings on the lower surface on practically all segments aid in this action. These swellings are armed with many fine hooks which serve for anchorage as the larva moves. The hooks are in transverse rows, unevenly arranged, as can be seen in figure 16, a photomicrograph showing distribution on one of the swellings.

The muscles of the larva are arranged as a casing just below the skin. The dorsum is covered by stout muscles cross-hatching in the segment, as can be seen in figure 17. These muscles as arranged, however, leave an open diamond on the midline, as can be seen in the illustration. By reason of this, the beating of the heart may be seen through the
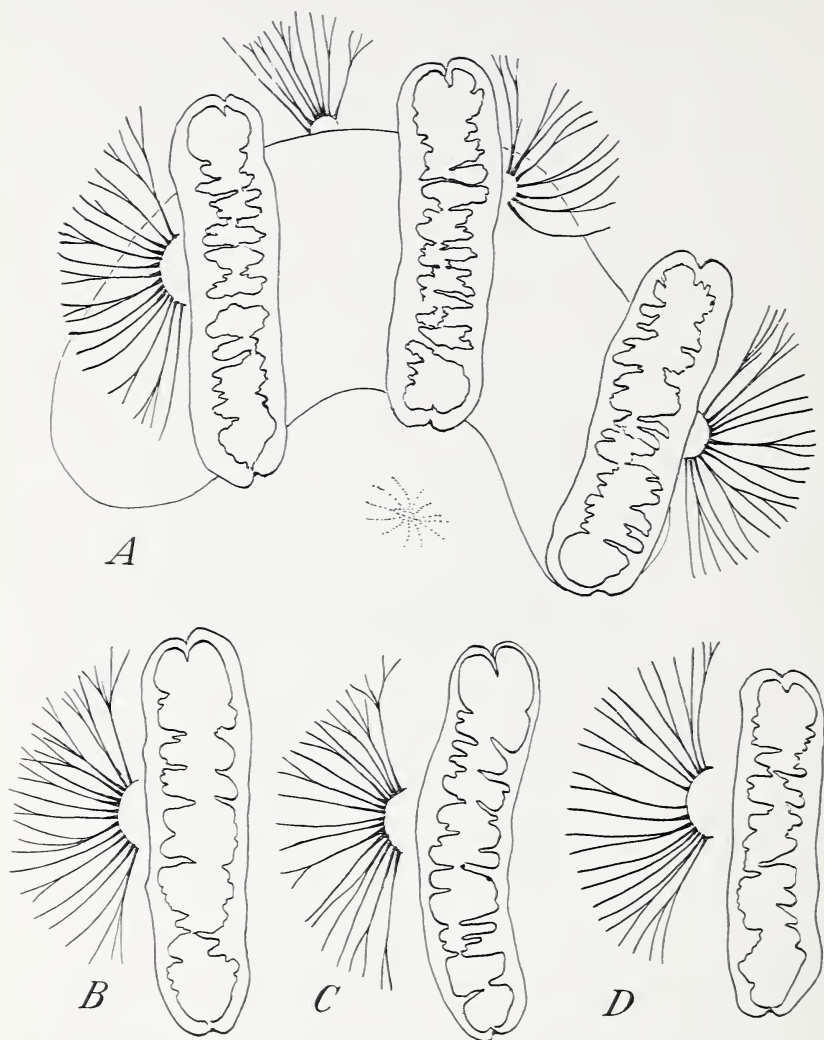
FIGURE 14.—First spiracles of *Anastrepha ludens: A*, Spiracular plate from larva of 1933; *B*, first spiracle of larva taken from mango in 1932; *C*, first spiracle of larva taken from sweet pepper in 1937; *D*, first spiracle of larva taken from citrus in 1937.

FIGURE 15.—Larva of *Anastrepha ludens* showing details.

transparent dorsal body wall. The sides possess three series of muscles at the intersegments extending upward at different angles toward these dorsal obliques, and other series extending downward at an angle toward the ventral muscles. On each side of each segment, also, there is a series of short dorsoventral muscles in the middle of the segment. Along the venter on each side is a series of longitudinal muscles. From the location of these, cross-hatching obliques, more slender than those on the dorsum, arise forming a pattern below with a more or less open central spot on each segment. The muscle arrangement, therefore, permits the larva to move in almost any direc-

FIGURE 16.—Photomicrograph of hooks on the foot swelling of a larva of *Anastrepha ludens.*

tion, to travel with some speed, and to burrow quickly into the ground for purposes of pupation.

The mouth is composed of a longitudinal cavity, in which the two strong mouth hooks are located. These work in an up-and-down movement and thus permit the larvae to do great damage in a fruit. Only the outer portion of the hooks protrude from the mouth, as can be seen in figure 15. The bases of these hooks, however, are articulated with the pharyngeal skeleton as shown in figure 18. The shape of these hooks and the form of the skeleton are sometimes used as an aid in differentiating larvae of different species. The pharyngeal skeleton is doubled like a folded leaf, with an articulation and its hook

on each side. The esophagus enters the cavity thus formed from the rear. Tracing it backward, it passes to the proventriculus, just behind which, at its junction with the intestine, small gastric caeca are located. The intestine opens at the knoblike structure seen at the rear of the larva.

The posterior breathing slits, or spiracles, have been already mentioned. The respiratory apparatus differs very definitely from that of the adult, functioning by means of two dorsal trunks which extend,
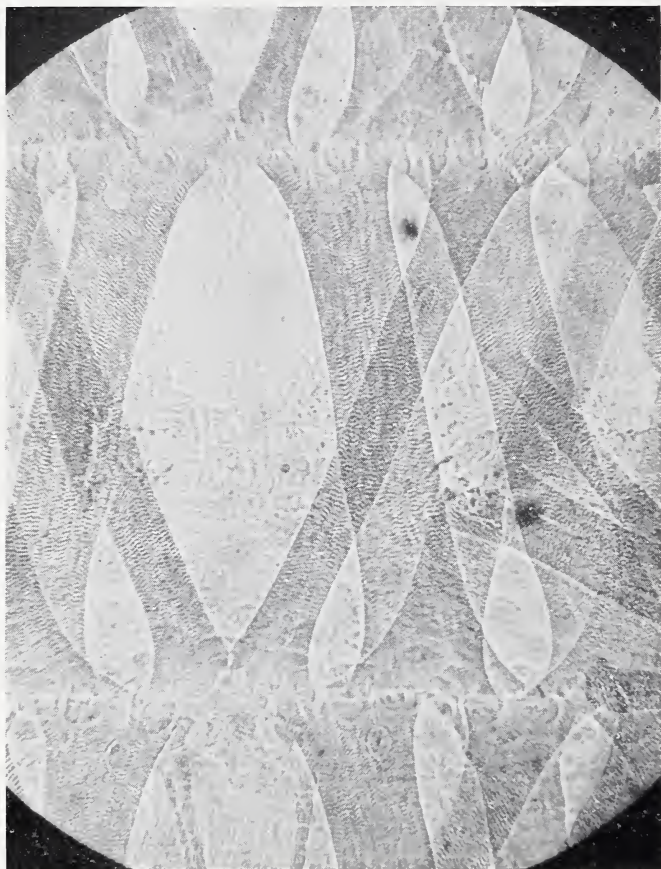
FIGURE 17.—Arrangement of dorsal muscles of larva of *Anastrepha ludens* which permits a record of the heart beats as a mortality end point.

one on each side, from the posterior spiracles to the anterior spiracles. These last are shown in figure 19. The "beads" which arm them differ in general number and arrangement in different fruitflies and aid in distinguishing the species. However, the number varies in different individual larvae of *Anastrepha ludens*.

A knowledge of the respiratory processes of the larva is of considerable importance in the perfection of methods of control so that its study therefore becomes necessary, but this review is not the place

for a technical discussion of those processes. It is well to point out, however, that the respiratory system possesses a main anterior and a main posterior dorsal commissure as well as minor segmental ones and also lateral intersegmental connections which apparently do not reach

FIGURE 18.—Mouth hooks and articulations of larvae of *Anastrepha ludens:* A, Mouth hook and articulation of first instar; B, mouth hook of second instar; C, mouth hook of third instar.
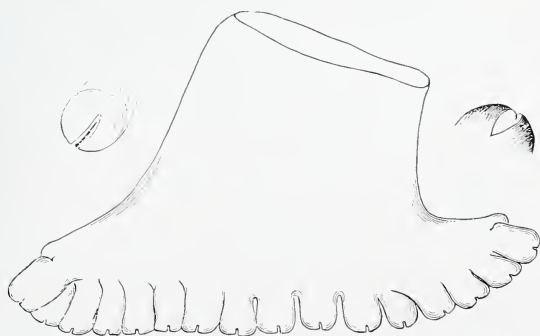
FIGURE 19.—Anterior spiracle of larva of *Anastrepha ludens.*

the exterior. These latter, or ones corresponding to them, are the functioning elements in the adult, which possesses lateral spiracles on the abdominal segments, including a pair on the ovipositor sheath of the female.

The circulatory system is simple. The heart is a dorsal tube supported in a diaphragm and visible between the breaks in the muscular system previously mentioned. No extended study has been made by the authors of heart action, but, owing to its nature and to the fact that it is easily observed, heart beat has been used in refrigeration and other studies to mark the end points in mortality.

The sensory organs shown on the tip of the head in figure 15 are very greatly enlarged in figure 20. They are of three kinds; and, since organs similar to them are located in the same places in other fruitflies, they obviously have selective functions in the life of the larva. Just what these functions are is not known at present. On the outer prominence the lateral one stands out considerably from the surface with a double shoulder and has in the center a rounded, projecting, hyaline cone. The second one on this prominence shows at the surface only as a sort of disk with projections from it that appear to be compound or striated. On the inner prominence the structure is externally a broad-based cone with a crater containing sharp, stout pegs. The two first discussed are connected below with large flask-shaped bodies.

Length of Life Within Fruit

The period of time spent within a fruit includes that of the egg stage after deposition and that required for development of the larva. Crawford estimated the incubation period at 4 days. Bliss and McPhail [57] found it to range from 5.5 days to 9.5 days with a mean of 7.67 ± 0.08. The duration was largely dependent on temperature. Later McPhail and Bliss (*29, p. 7*), studying the incubation of 1,730 eggs, obtained a duration of from 6 to 12 days and plotted the bulk of their data as shown in figure 21. The work was done under natural variation of temperature.

These workers [58] determined the duration of the larval period in Cuernavaca, using watch glasses containing pieces of cut mango renewed every other day. They obtained a range of from 18.5 to 35 days. The temperature varied with the period, but the mean was 70.52° F.

They had no way to obtain uninfested mangoes so they held mangoes from date of collection until the emergence of the last larvae, and in this way determined the longest egg-larval period available to them in the field. This proved to be 44 days. During the same period as previously mentioned, they had studied incubation, obtaining the longest duration as 9.5 days. This, added to the longest duration for the larval stage obtained experimentally, gave $9.5+35=44.5$ days, an experimental figure in very good agreement with the 44 days maximum from the holding of field mangoes. It may be assumed, therefore, that the experimental figures obtained are of suitable accuracy. Crawford (*8, p. 177*) had previously indicated that the larvae leave the fruit in about 6 weeks, his time interval, therefore, presumably including that of incubation.

In studying the reactions of the larvae to vapor sterilization of fruit, Stone, as will be discussed later, found a difference in the time required by that process to kill in different fruits. He therefore undertook a study [59] of the length of time required from oviposition to

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[57] See manuscript report 8, p. 152.
[58] See manuscript report 8, p. 152.
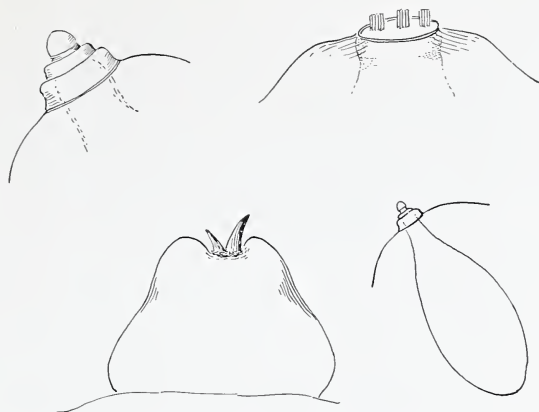[59] See manuscript report 47, p. 153.

FIGURE 20.—Sensory organs on tip of head of larva of *Anastrepha ludens.*
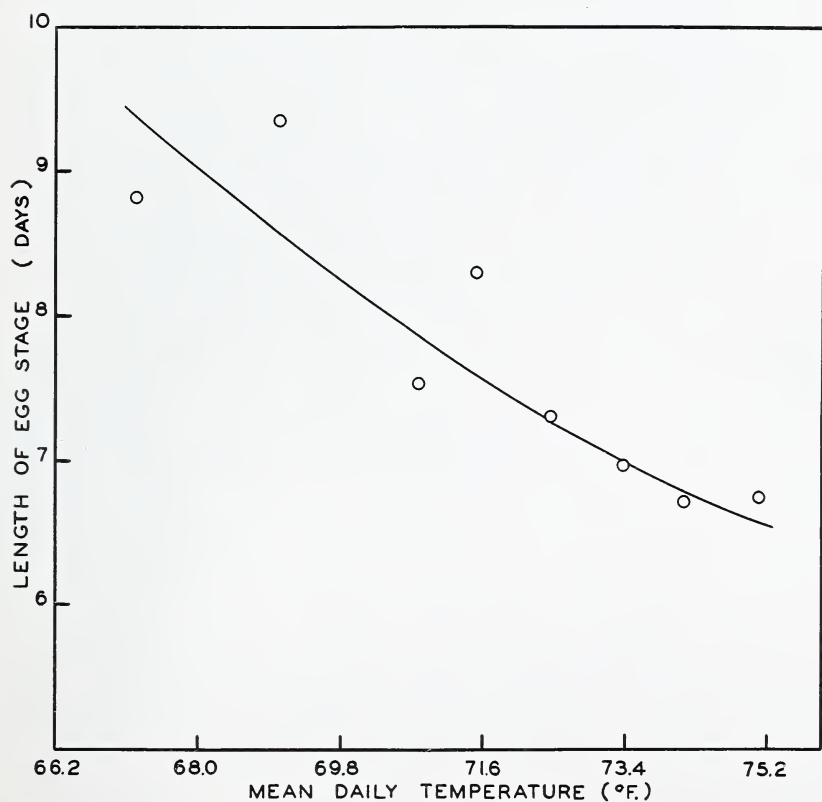

FIGURE 21.—Duration of egg stage of *Anastrepha ludens* in relation to tempera-
ture.   (After McPhail and Bliss (*29*).)

larval maturity in different fruits. He selected 77° F. as probably near the optimum temperature. Fruits were exposed to mature females for a period of 2 hours and were then held under identical conditions in the large conditioning room in the laboratory until larval maturity. Mangoes were first sterilized, since no source of uninfested mangoes existed. Conditions were made as uniform as possible.

The results gave a striking difference with different fruits, the figures ranging from 15 days in figs to 32 days in mandarins (table 2). It should be understood that these data represent the first maturity in each case, or in other words the minimum time required for each fruit. A direct comparison cannot be made with the figures of McPhail and Bliss, since the mean temperatures to which their material was subjected never ranged above 75° F., even for the eggs. In Stone's results, however, there was some variation in duration within the puparium, possibly indicating a carry-over of the effect from larval feeding. This will be discussed later. However, since Stone's puparia from sterilized mangoes required incubation for 17.6 days at 77° F. in the conditioning room, in which temperatures vary somewhat, and since Darby and Kapp obtained minimum length of life of puparia from mango in 17 days at a closely controlled temperature of 76.1° F. in incubators, it is probable that development in the sterilized fruits was approximately normal.

TABLE 2.—*Influence of different fruits on the duration of larval life of Anastrepha ludens at 77° F.*

Fruit	Lots studied	Minimum time to formation of puparium	Shortest time spent in puparium	Total time to emergence of first adult
	Number	*Days*	*Days*	*Days*
Fig	1	15	17	32
Mango	9	15.6	17.6	33.2
Chili pepper	1	16	18	34
Apricot	1	18	17	35
Bell pepper	2	16.5	19.5	36
Bumelia laetevirens	5	19	16	35
Calabaza	1	20	16	36
Tomato	1	20	19	39
Spondias mombin	1	20	19	39
Peach	1	20	22	42
Pitaya	1	22	20	42
Banana	1	23	19	42
Grapefruit	16	25.9	18.4	44.3
Pear	1	26	18	44
Orange	35	27.2	19.1	46.3
Apple	30	30.4	22.4	52.8
Mandarin	1	32	18	50

As a general rule, the shorter the period for fruit maturity the more rapid was the development of the larvae—a parallel that would no doubt hold if very similar varieties of widely different dates of maturity could be compared. This correlation between some factor or factors in fruit maturity and larval maturity offered an interesting problem, but time has not yet been available to attack it.

In Stone's experiments sour lime was infested on exposure to adults, but owing to the fact that nothing had emerged for many weeks he opened the fruits and found larvae, still very small, unable to make progress against the adverse conditions. These larvae ultimately

died.   Darby [60] gave comparative measurements of the hydrogen-ion concentration in 6 fruits, the range in sour lime in 30 cases being from pH 2.0 to 2.2.   This he considered too low for larval development, since larvae transferred from sweet lime or mango to slices of sour lime showed extreme irritability and ultimately died.   Acidity, therefore, may be the inhibiting factor in sour lime.   Crawford (10, pp. 378, 379) transferred larvae from grapefruit to lemons, where they lived for several weeks and ultimately produced adults, thus showing that lemon is not too acid for survival when larvae of some size are introduced.

Comparing the brief time required for larval maturity in mango and the long duration before death in sour lime, it might be concluded, as previously mentioned, that fruits giving the shortest maturity period for the larvae are the most suitable.   Figs, however, require less time than mango but seem to be of no great importance in nature, while, on the other hand, grapefruit requires a relatively long period. From data available, therefore, it is scarcely possible at the present time to indicate the optimum larval environment.

Darby and Kapp (14, p. 3) gave data showing a decreasing pH value associated with increasingly longer time before pupation, from pH 8.7 in 5 days to pH 4.5 in 17 days.   This evidently is in keeping with the extended duration of larval life in lemons and limes.   It is possible, therefore, to group fruits according to the pH readings of the pulp or juice, and against this to compare the length of time within the fruit found in Stone's studies just discussed.   The first group includes the sour limes and lemons, which need not be listed. Other examples are given in table 3.

TABLE 3.—*Duration of larval life of Anastrepha ludens in different fruits in relation to the acidity of the fruit juice*

Host	Range of acidity	Worker	Duration
	pH		*Days*
Bell peppers	6.0–6.6	Julia Baker	16.5
Fig	4.4–5.8	____do	15
Common mango	3.8–4.2	Darby [1]	
	3.5–4.3	Julia Baker	15.5
Orange—Valencia	3.8–4.2	Darby [1]	
	3.2–4.7	Julia Baker	27.2
Grapefruit	3.1–4.4	____do	25.9

[1] Manuscript report 10, p. 152.

While citrus as a group gives rather low pH measurements and has as a group a rather long larval developmental period within the fruit, there appears to be no uniform relation between larval duration and pH value as a whole, and the mango is quite out of line with the gradient given by Darby and Kapp.

The question of the variation among fruits as regulated by temperature is an economic one, since larval duration would influence the number of generations in every locality; accordingly, to compare with his extensive data at 77° F., Stone [61] undertook work at both higher and lower temperatures.

[60] See manuscript report 10, p. 152.
[61] See manuscript report 72, p. 154.

To make a comparison in material that could be obtained unin-
fested in quantity he utilized peppers. At 59° F. the shortest larval
duration was 54.25 days, and at 68° it was 25.5 days. At 77° it
was 16.5 days and at 86° it was 14 days.[62] These figures represent
the shortest duration in different lots at the same temperature. The
results are shown in figure 22. This figure, like figure 32, shows
that 86° is above the range at which temperature response is regular,
and that predictions for the egg-larval period as for the pupal period
cannot be carried, on a simple basis, to such high temperatures.
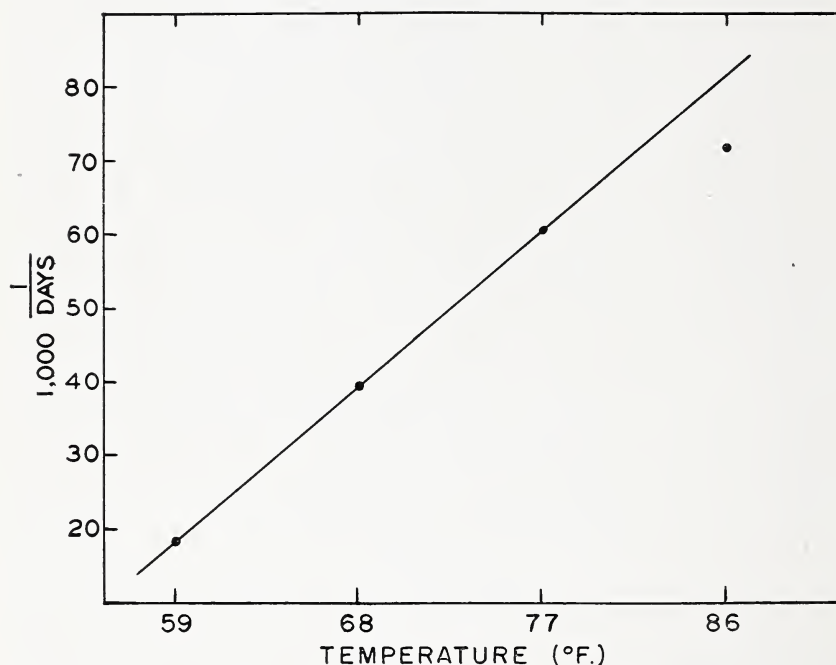
FIGURE 22.—Relation between temperature and length of combined egg and
larval periods of *Anastrepha ludens* in pepper.

Methods for Destroying Larvae in Fruit

Many methods have been discussed at various times as possibilities
for killing larvae and eggs within fruit without injuring it and
thus assuring its safety for shipment to areas free from the fruitfly.
Nearly all these have had their inception in the fact that the move-
ment of fruit has been restricted. The first attempts to kill larvae in
fruit were in Mexico. Santillan, in Herrera et al. (*21, p. 11*), at-
tempted to use electricity and experimented also with larvae in oranges
that had been opened. In Florida experiments were carried out
with fruit infested with the Mediterranean fruitfly, and these have
given information valuable to the work with *Anastrepha ludens*.
For example, studies there by McBride [63] showed that X-rays could
not be used. Efforts to use chemical solutions of various kinds also

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[62] See manuscript report 84. p. 155.
[63] See manuscript report 9, p. 152.

proved them to be ineffective. Baker in Mexico did preliminary work in the zone of short radio waves and did experimental work with infrared, and, while interesting results were obtained with adults, the use of such methods for the sterilization of fruit was indicated as impracticable. The only remaining methods which appeared workable at the time were the vapor-heat process developed in Florida (47) and the refrigeration method also perfected there during the campaign against the Mediterranean fruitfly [64] (48). Fumigation methods are under investigation, but results are not yet available.

LARVAL MORTALITY AT HIGH TEMPERATURES

The first recorded studies on the effects of high temperatures on *Anastrepha ludens* were conducted by Herrera and his associates (21, p. 77). These were made in an effort to prove that the insect would not become injurious in the United States.

Later Crawford (8, p. 194), did the first experimental work with the effect of heat as a treatment, using infested fruit in a steam heater and in banana-ripening rooms, and proposed that a heat treatment in rooms similar to banana-ripening rooms might be utilized for release of fruit under embargo in Mexico. As a result of his experiments he reported 110° and 115° F. as satisfactory lethal temperatures and thus opened the way for subsequent detailed studies.

In 1927, when the Mexican fruitfly was found in Texas, Baker,[65] citing these Mexican results in a program of work, proposed the perfection of a high-temperature process as a safeguard, but the studies outlined were not undertaken until the appearance of the Mediterranean fruitfly in Florida in 1929.

The program for the Mexican laboratory [66] called for specific thermal death-point studies, and the first reported results were presented by Darby,[67] in January 1929 and supplemented later.[68] Darby's data provided the first systematic death-point records on larvae of *Anastrepha ludens*. His work was done in hot-air incubators. In an effort to obtain uniform results he adopted the technique of exposing larvae in Petri dishes with a little mango pulp. In April 1929, however, he and Kapp [69] presented an 8-hour curve and a 4-hour curve in whole mangoes. These curves are shown in figure 23.

After the perfection of the vapor-heat sterilization process in Florida, Darby and Kapp[70] presented data at 110.48°, 108.86°, and 104.9° F. Figure 24 is a mortality diagram prepared from their data for 104.9° F. The regression line is represented by the formula $Y = 5.618 + 10.124 \ (X - 1.059)$, where $Y =$ mortality in probits and $X =$ time of exposures administered (in logarithms). It indicates that at 25 hours a satisfactory "complete kill" would be expected (99.997 percent). This work was of a preliminary nature, 100 larvae being used at each exposure point. Experiments with 500 larvae by the

[64] See manuscript report 77, p. 154.
[65] See manuscript report 3, p. 152.
[66] See manuscript report 5, p. 152.
[67] See manuscript report 11, p. 152.
[68] See manuscript report 12, p. 152.
[69] See manuscript report 15, p. 152.
[70] See manuscript report 29, p. 153.

same workers at 108.86° reached the same level of mortality, as estimated graphically, in 20 hours, and others with 400 larvae at 110.48° in approximately 5 hours. These experiments were also done in incubators.

The work was next taken up by Baker and Stone, who obtained no survival at 4 hours at 110° F., but at 4¾ and 5 hours survival occurred. Variability at the higher temperatures was traced to temperature differences in locations within the incubators. On marked spots 685 larvae at the 5-hour point at 110° F. gave no survival. No further
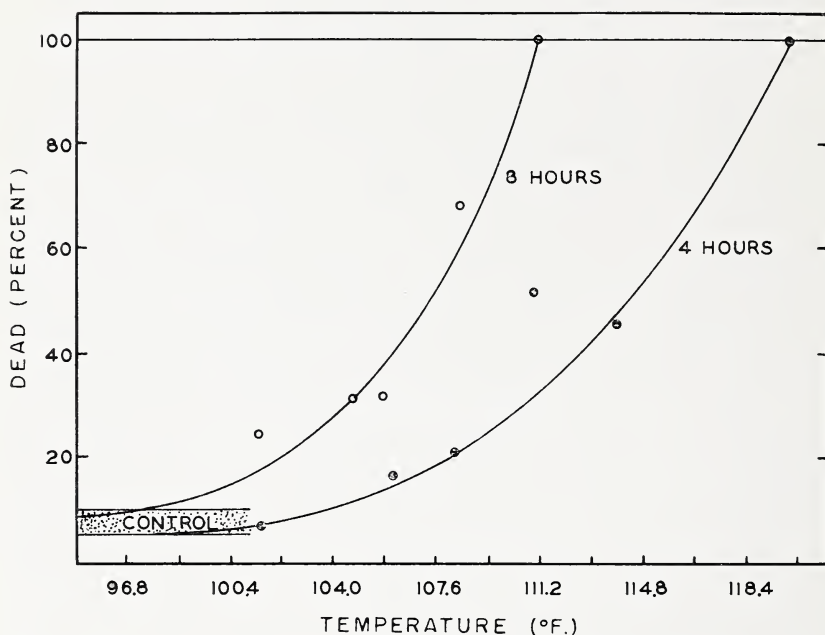
FIGURE 23.—Mortality of larvae of *Anastrepha ludens* when subjected to different high temperatures for 4 and 8 hours. (After Darby and Kapp (13).)

work of this character was done, but attention was turned to experiments in which the vapor-heat process was used in a standard cabinet installed for this purpose.

THE VAPOR-HEAT PROCESS OF FRUIT STERILIZATION

The first experiments in Mexico in which the vapor-heat process, as such, was used were conducted by Stone[71] in 1932. This process was perfected in Florida in 1929 during the campaign against the Mediterranean fruitfly. It is dependent on the circulation of air, saturated water vapor, and water in the form of a fine mist, in large volume throughout the load. Saturated vapor is essential in order to obtain the desired mortality and to produce temperature equilibrium. In the development of the process the work of Crawford was utilized as an indication of suitable temperature and the 1929 death-point curves of Darby and Kapp as an indication of required duration.

[71] See manuscript report 39, p. 153.

Thus the first work in which the latent heat of saturated vapor was specifically utilized for the sterilization of fruit infested by fruitfly larvae was conducted in Florida by Yothers and his assistants under the senior author's direction. After the laboratory perfection of the process, its commercial application, in which A. Gordon Galloway played a major role, was mainly carried out under the direction of Lon A. Hawkins.

Darby's [72] (13) death-point curve for *Anastrepha ludens* had indicated "complete mortality" at 8 hours at a little above 110° F., and the fruit-sterilization experiments in Florida had centered around 8 hours with fruit infested by *Ceratitis capitata* and with all types of sound fruit. Ultimately an 8-hour exposure had been there adopted in the vapor-heat process. Since, however, the death-point studies by Darby could give no information on relative mortality in the approach period as compared with the exposure period during vapor sterilization of fruit, a differentiation early made by Yothers, Stone undertook a check on this point with larvae of *Anastrepha ludens*. The first run was for 5 hours, with an approach of 3 hours and 10 minutes, using whole oranges containing 1,478 larvae; the second was for 6 hours, with an approach of 6 hours and 45 minutes, using oranges with 1,659 larvae; and the third was for 7 hours, with an approach of 9 hours, using both oranges and mangoes and 2,733 larvae. Mortality was complete in all three cases.

Further studies [73] covered in all 11,712 larvae. The temperature was held at 110° F., while the exposure periods ranged through 3¾, 4, 5, and 5½ hours. No living larvae were obtained at 4 hours or longer, and only 3 out of a total of 1,792 survived at 3¾ hours. In these runs, however, the approach period ranged from 4 hours and 52 minutes to 12 hours and 2 minutes.

Stone therefore conducted further studies at exposures of 3¾, 4, 5, and 5½ hours, with the approach held constant at 8 hours, the standard approach time adopted in Florida. By hourly withdrawals from the sterilization cabinet during the approach period he was able to determine mortality during that period.

The following year Stone [74] returned again to this problem, using 24,750 larvae and recording the mortality, as before, at 1-hour intervals during the process. Mangoes and oranges were recorded separately, with the result that quite a different mortality during approach was obtained in the two fruits. The fact that oranges gave somewhat different results from mangoes and that mortality therein was very high during the approach period led him to further studies,[75] using 28,375 larvae, the fruit being treated at 5 hours with an approach of 8 hours. Complete mortality was obtained. It seems fairly safe to conclude, therefore, that the vapor-heat process applied to oranges at a temperature of 110° F., with an approach period of 8 hours and an exposure period of 6 hours, will guarantee the death of any larvae or eggs that may be present in the fruit, even if the population should be relatively large (44).

In all these studies saturated vapor was maintained throughout both the approach period and the exposure period. The few experi-

[72] See manuscript report 25, p. 153.
[73] See manuscript report 39, p. 153.
[74] See manuscript report 41, p. 153.
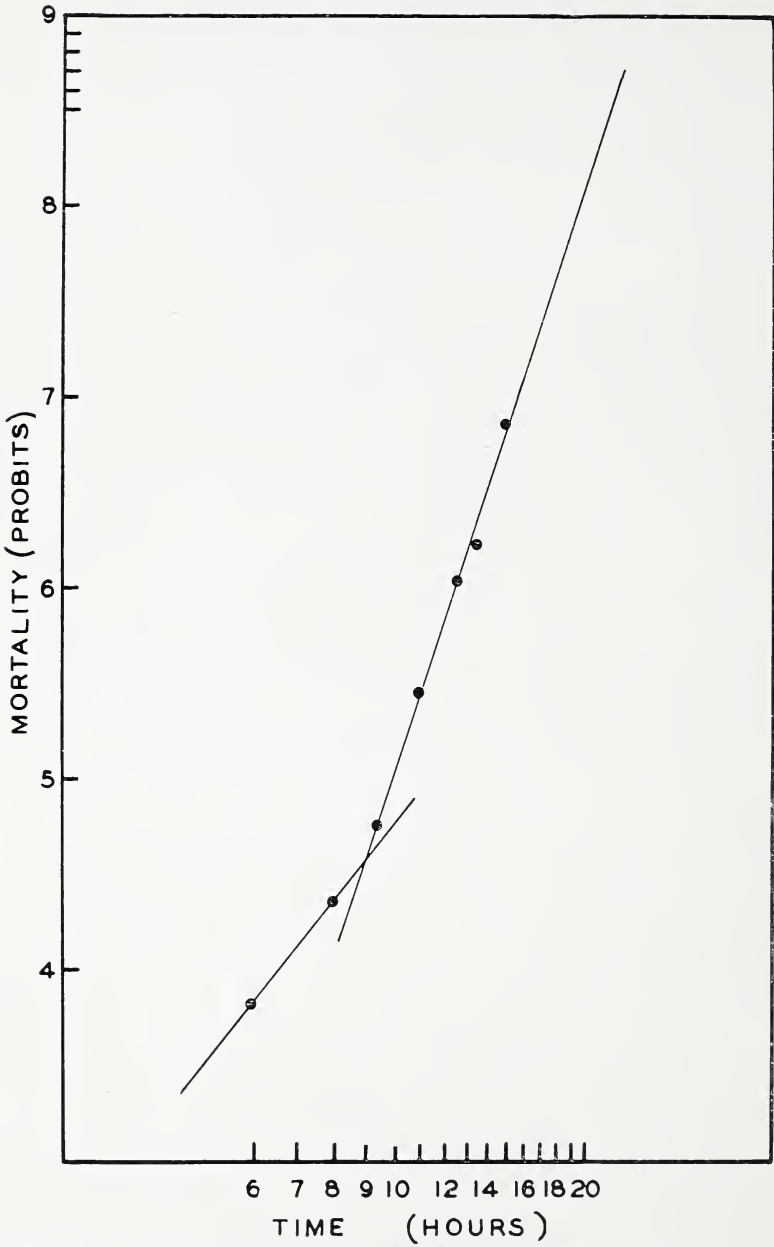[75] See manuscript report 43, p. 153.

FIGURE 24.—Mortality of larvae of *Anastrepha ludens* when subjected to a temperature of 104.9° F. (Data from Darby and Kapp (*13*).)

ments in which accidents made this impossible were at once discontinued. The original experiments in Florida had shown saturated vapor to be one of the major requirements. Since both the resulting mortality and temperature equilibrium throughout the load are largely dependent on it, no experiments were conducted with *Anastrepha ludens* to measure the reduction in mortality that would follow the use of superheated vapor. The treatment for 6 hours at 110° with an approach of 8 hours is therefore dependent on the use of saturated vapor throughout the treatment. A mixture of air, saturated vapor, and water mist is used.

Stone, in his work at 110° F. which compared larvae of *Anastrepha ludens* in orange and mango with those of *A. striata* in guava, found differences in mortality during the 8-hour approach period, the mortality rate of *A. striata* being slower, although there was no apparent survival in any lot after exposure had reached 110° F. for 4 hours. All *A. ludens* were dead at 3 hours, but some *A. striata* in guavas had survived the 3 hours and succumbed at 4 hours. This indicated either that *A. striata* is more resistant than *A. ludens* or that guava as a host fruit causes a greater resistance in larvae. The latter point could not be attacked directly, since *A. ludens* and *A. striata* are not exchangeable as to host fruits.

However, the curve for *Anastrepha striata* in guava, as opposed to those for *A. ludens* in other fruits, indicated an expected survival at 5 hours. On the basis of the curves, therefore, *A. striata* appeared more resistant. Stone, as a result, treated 1,240 guava fruits, containing 2,360 larvae of *A. striata*, for 5 hours, with an approach of 8 hours. The fruits were run in 2 lots and in neither lot were surviving larvae found but in each lot one puparium had been formed inside a guava fruit. One puparium failed to produce an adult, but a male emerged from the other. Survival at 5 hours was proved. Since survival of *A. striata* from a population of 2,360 was obtained and no survival of *A. ludens* from a population of 28,375, to mention only the one series, it seems evident that *A. striata* is more resistant than *A. ludens*.

The question was attacked also from another angle in connection with another problem. As discussed earlier, Stone had found a wide variation in the time required for the development of *Anastrepha ludens* in different fruits under the same temperature conditions. Orange was one of the fruits requiring the longest period, and mango one of those requiring the shortest. It became pertinent, therefore, to inquire if this variation bore any relation to mortality during sterilization. Pepper, although an artificial host, is another fruit with a shorter time period for larvae than that of orange. Stone[76] therefore conducted sterilization experiments in which mortalities in these three fruits, both during the approach period and during the exposure period, were compared. His graph showing the results is given in figure 25.

It will be seen that there is a definite relation between the duration of the normal larval stage in a fruit and the mortality during the approach period during sterilization of that fruit. Orange, with the longest period, gives the most rapid mortality. Mango, with the

[76] See manuscript report 67, p. 154.

shortest, gives the slowest mortality, and pepper, which is intermediate, falls between. While this variation during the approach is shown, as was the case with *Anastrepha striata* in guava and *A. ludens* in orange, it will be noted, on the other hand, that complete mortality in all three cases with *A. ludens* was obtained at 4 hours' exposure. This last study, therefore, not only brings out the interesting correlation discussed, but again supports the opinion that *A. striata* is more resistant to these conditions than is *A. ludens*.

In this connection, also, Stone [77] used 2,665 larvae in Petri dishes containing small amounts of buffered solutions ranging from pH 2.65 to pH 7.49. The resulting data appeared to show that hydrogen-ion concentration is of no great importance during the actual process of sterilization itself.
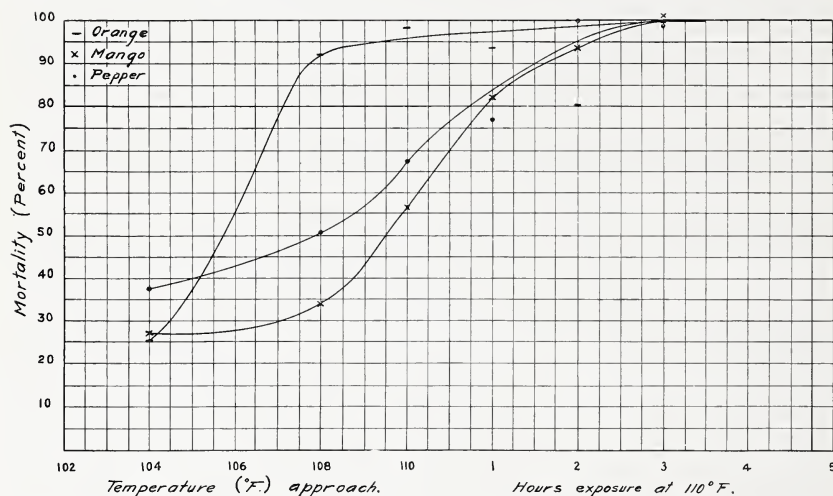
FIGURE 25.—Mortality of larvae of *Anastrepha ludens* during approach period in vapor-heat sterilization experiments in which orange, mango, and sweet pepper were used. Based on examinations of lots of fruits taken hourly from the chamber.

The reaction of citrus varieties and many other types of fruit to the vapor-heat process was studied in detail in Florida. And it is well to remember that fruit produced under different climatic conditions responds very differently to different methods of treatment and handling. In Mexico the authorities had established interior quarantine zones restricting the movement of fruits from heavily infested zones to those of light infestation. An interest developed, therefore, in the possibility of using vapor-heat sterilization before releasing fruit to the zones more lightly infested.

As a result, experimental work was planned on oranges and mangoes, the Mexican Department of Agriculture supplying the fruit and making the holding studies while the Bureau laboratory in Mexico City conducted the actual sterilization. The sterilization experiments were handled by Baker with the assistance of Ramírez. The holding and related studies were conducted by Pablo Hope y Hope of the

Mexican Instituto Biotécnico. Oranges, including one lot of navels, were obtained from several localities. The oranges, when received, were very variable in quality and degree of maturity, and it was impossible to obtain data on the dates of picking, the methods of handling, etc., prior to treatment. Results from the treatment as far as fruit quality is concerned were therefore very variable, and in the senior author's opinion only the treated navels appeared indistinguishable from the controls. Mexican workers who sampled the treated fruits considered most of them satisfactory. After treating a considerable number of lots it was decided that adequate data on response to the treatment could be obtained only from samples with completely known history, and that some other procurement procedure would be essential if this information were to be obtained.

Experiments with mangoes suffered from the same cause. Sometimes these fruits would arrive green and hard, at other times over-ripe, so that consistent studies could not be made. Here also the question of variety or local fruit variation entered. One interesting result with the mangoes, however, appeared to be consistent. The treated fruit held up for considerable periods, tending slowly to mummify rather than to rot, in contrast with the controls. The work was suggestive, but indicated that for satisfactory results experiments should be made at the sources of production where the fruit might be gathered and handled according to definitely prearranged plans.

In the application of the vapor-heat process of fruit sterilization, several things are necessary. Saturated vapor must be obtained at the temperature used throughout the approach period, since it has an important effect on mortality and since latent heat by condensation is utilized to obtain temperature equilibrium throughout the load. Saturated vapor must be maintained also throughout the treating period to prevent cooling by evaporation from the surface film on the fruit. Adequate circulation capacity is required to move the air-vapor-mist mixture in sufficient volume throughout the load. Temperature of the entering mixture must be closely controlled. With these conditions fulfilled, excellent experimental results have been obtained. Flabby fruit has become more turgid. Latent injuries have become apparent. Chemical composition has not been noticeably altered. The operating cost is low, and the method is relatively rapid.

It is worthy of mention also that sterilization equipment controls closely those factors on which "coloring" is dependent, so that such equipment is of excellent service for that purpose.

THE REFRIGERATION PROCESS OF FRUIT STERILIZATION

During the progress of the early work by Back and Pemberton (*1*) on the Mediterranean fruitfly in Hawaii, studies were made on the effects of cold-storage temperatures on larvae within fruit with the idea of the possible utilization of cold storage as a method of fruit treatment. This work was extended in Florida and later in Hawaii by Yothers and Mason [78] during the campaign against *Ceratitis capitata* in the United States, and refrigeration as a sterilization method was authorized for the release of fruit for shipment (*46*, *48*).

[78] See manuscript report 19, p. 153.

Owing to the urgent need of a low-temperature method in the Rio Grande Valley of Texas, Stone and Baker,[79] with the assistance of Ramírez, undertook the problem in Mexico using over 50,000 larvae, basing the work on the results with *Ceratitis capitata*. Readings were made on fairly normal puparium formation. A low-temperature method using a temperature of 30° to 31° F. was approved in 1932 (*49*) and applied at that time to about 214 carloads of citrus. An exposure of 15 days was adopted, following the policy of extra safeguard employed in the temperature recommendation for the Mediterranean fruitfly in Florida. However, no adults emerged after 10 days in the experiments, and subsequent experience with higher temperatures supports the conclusion that the exposure time at 30° to 31° F. may be reduced.

The experiments showed survival of larvae, as indicated by heart beat, after exposures up to 47 days, but at the longer exposures puparium formation did not occur. On the thirteenth day one individual out of 1,552 larvae made a fairly successful attempt to pupate. This puparium, however, did not survive.[80]

With the purpose of developing methods of treatment more nearly within the range of commercial practice, work was continued at 32° to 33°, 33° to 34°, 34° to 35°, and 35° to 36° F. The experiments at the highest temperature range, 35° to 36°, undertaken by Stone and Shaw, are still under way at the time of writing. Those at the lower ranges, largely carried out by Stone, make it possible to select exposure times with approximately equal security at the different temperature ranges.

The resulting exposures arrived at are 18+ days at 32° to 33°, 20 days at 33° to 34°, and 22+ days at 34° to 35° F. Last survival in the experiments themselves was on the sixteenth day at 32° to 33°, on the seventeenth day at 33° to 34°, and on the sixteenth day at 34° to 35°. The series at 33° to 34°, based on a population of 60,146 larvae, as estimated from a partial count, was the most extensive and indicated that last survival at 34° to 35° was at an unexpectedly short exposure. Variability in all series led to the decision to adopt a line based on the greatest survival. This is illustrated in figure 26, where only the outside points for *Anastrepha ludens* are used.

Exposures like 18, 20, and 22 days show conclusively how resistant *Anastrepha ludens* larvae are to low temperatures, and it is interesting to compare the results on *A. ludens* at 33° to 34° F. with those on *A. mombinpraeoptans* and on *Ceratitis capitata*. Data gathered by McAlister[81] at 34° F. with *A. mombinpraeoptans* and data recorded by Mason[82] at 36.5° with *C. capitata* show these two species to be much more susceptible than *A. ludens*.

The 3 lines representing mortality are compared in figure 26, and striking differences are at once apparent. With both *Anastrepha ludens* and *A. mombinpraeoptans* the lines are drawn on emergence of adults. With *Ceratitis capitata*, however, the data are on formation of puparia. Therefore the comparison is much less strict with the Mediterranean fruitfly, and that species is more susceptible than the comparison of the lines themselves would indicate. The line for

[79] See manuscript report 37, p. 153.
[80] See manuscript report 46, p. 153.
[81] See manuscript report 70, p. 154.
[82] See manuscript report 74, p. 154.

C. capitata was drawn from an estimated population (*2, p. 6*) of 90,826 larvae and that for *A. mombinpraeoptans* from an estimated population of 71,470, whereas, as previously mentioned, an estimated population of 60,146 larvae was used in the experiments with *A. ludens.*
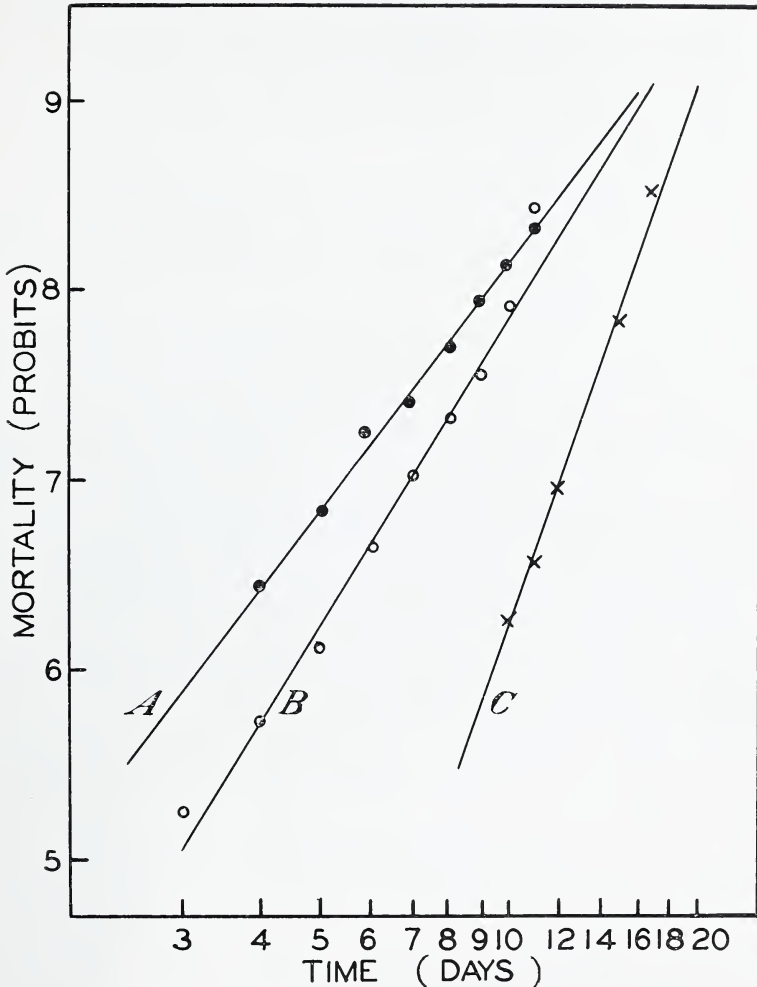
FIGURE 26.—Comparisons of mortality lines: *A, Anastrepha mombinpraeoptans* at 34° F.   (Data from McAlister, No. 70 in Manuscript Reports Cited.) ; *B, Ceratitis capitata* at 36.5° F.   (Data from Mason, No. 74 in Manuscript Reports Cited and Baker (2).) ; *C, A. ludens* at 33° to 34° F.

Sterilization by refrigeration is a relatively expensive process and obviously requires time.   It could scarcely be counted on for the rapid movement of a crop.   But at the end of a season, where storage is normally indicated, it often may be used to advantage in conserving for a later market fruit that otherwise could not be moved.   Refrigeration methods are so well known that they require no comment here,

Factors Causing Larvae to Leave Fruit

In 1928 McPhail and Bliss (*29, pp. 8-11*) showed that larvae may remain in fruit for longer or shorter periods after reaching maturity. They found the factors responsible to be of two types, those independent of external influences and those dependent on modification in external environment. The factors of the first type still remain obscure, but at that time McPhail and Bliss determined several of the latter type which stimulate the larvae to leave the fruit. These are (1) gradually decreasing temperature, (2) rain or water falling upon the fruit, (3) shaking or jarring of the fruit, and (4) contact with moist soil rather than dry.

Of 1,032 larvae emerging from infested mangoes, more than 92 percent left the fruit before 9 a. m. In 6 lots of fruits more larvae appeared to emerge after cool nights than after warm ones. From fruit artificially and slowly cooled 61.4 percent of the larval population emerged, whereas from controls under a slowy rising temperature no larvae left the fruit.

Rain striking the fruit greatly increased emergence, thus reducing the time required for a generation of larvae to leave the fruit. Stone [83] has taken advantage of these findings to obtain larvae in very large numbers when desired. Ramírez constructed large bins, the sides sloping to a trough at the bottom. Each bin holds many bushels of infested fruit. When large numbers of larvae are desired, these bins are watered with a hose and the larvae, thus stimulated to emerge, are washed along the trough below and screened out for use.

McPhail and Bliss were inclined to interpret the stimulus to emergence by falling rain as a mechanical action due to the beating of the rain similar to the stimulus when mangoes were shaken, when a high percentage of the larvae contained at once emerged. It seems probable, however, that other factors are involved, since increased emergence is noticeable in Stone's bins during very heavy rains, even when these bins are protected from the falling rain itself.

Darby [84] gave hydrogen-ion measurements of sour lime, orange, sweet lime, guava, mango, and pomegranate. In his report he stated that when guava becomes more acid than pH 3.6, the larvae leave the fruit if possible.

Repeated observation confirms the fact that larvae of *Anastrepha ludens* do not mature in sour limes. Grapefruit and sour orange, however, are very favored hosts of *A. ludens* and in them large numbers of larvae mature. Were acidity of a range around pH 3.6 of real importance with *A. ludens*, larvae would not be found abundantly in these fruits. Interpreted in connection with suitability for the market, the outside acidity limits for fine-quality citrus would be about pH 3.2 to 4.2; grapefruit, however, is infested even while still green.

Methods of Fruit Disposal

Destruction of infested fruit in such a way as to insure the death of larvae or eggs contained in it is a matter of importance in any eradication campaign, or in grove sanitation under conditions of known infestation.

[83] See manuscript report 57, p. 154.
[84] See manuscript report 10, p. 152.

Much early work was done along these lines by the Mexican Commission of Parasitology during the campaign against *Anastrepha ludens* in 1900–1901. Large masonry ovens were constructed for the destruction of infested fruit, and burning was practiced extensively. Because of the fact that this was not always effective, De la Barreda (*21, pp. 187, 188*) at that time made a comparison between burning, burial, and immersion in water. Burial he considered excellent, if two points were observed, (1) a sufficient depth, and (2) prompt gathering of the fruit. The disadvantages he listed were (1) necessary size of pits where large quantities of fruit were concerned and their cost, (2) the slowness of the method, and (3) the necessity of daily digging of pits, for fruit was falling daily.

De la Barreda's experience with immersion showed that in 3 days decomposition of the fruit sets in and the larvae are destroyed. This work, however, was in a region of ample water supply, and mention is made of the fact that offensive odors resulted.

Tellez, in Herrera et al. (*21, p. 190*), made tests also, comparing burning, burying, and boiling in a 40-liter tank for 8 minutes, which latter he stated was sufficient to kill the larvae in mangoes. In these fruits they are relatively near the surface. He (*21, p. 291*) found that one laborer could handle by boiling 1,194 fruits per day; by burying, 2,388; and by burning, 1,668. He therefore recommended burial (under a depth of 50 cm. of earth) as the cheapest and safest method of fruit disposal.

In 1927 the senior author found in the Rio Grande Valley of Texas that if fruit were buried completely under a depth of 18 inches of soil and somewhat tramped, no flies emerged in screens placed over the burial spots; hence this method of disposal was recommended at that date as suitable.

Full studies on the effectiveness of burial at different depths in different kinds of soils were undertaken with the establishment of the Bureau laboratory in Mexico City. McPhail and Bliss (*29, p. 15*) found that adults emerged through 18 inches of coarse, unpacked soil, and that twice as many emerged from different depths from 1 to 18 inches when the burial pits were located in the shade as when they were in the sun. An analysis of the data by McPhail [85] indicated that 75 percent of the emergence was accounted for either by conditions of depth or sunlight. Darby and McPhail [86] found greatest emergence through fine soil if it were dry, but through medium or coarse soil greater emergence if it were moist, owing to the caking of the fine soil when moist.

Stone and Plummer [87] conducted a series of experiments comparing packed and unpacked soil, and Plummer and Stone (*35*) conducted a detailed study of the problem as a whole. They found that no adults emerged through 18 inches of packed soil, either dry or wet. During long, dry periods they often found fissures in the soil of the pits which might have facilitated escape of flies, and recommended burial under 18 inches of packed soil and periodic inspection of the pits to determine their condition.

The extensive data by Plummer and Stone are very instructive since they permit a study of the effect of soil at successive depths. As

[85] See manuscript report 18, p. 153.
[86] See manuscript report 17, p. 153.
[87] See manuscript report 28, p. 153.

the emergence of adults from pits of different depths might give a
misleading idea, the experiments were laid out to permit careful ex-
amination of the soil in each pit, 1-inch layers being removed and
studied at a time. This permitted a determination based on the
distances traveled upward by all the adults.

The unpacked series will be considered first. Flies emerged from
the 18-inch and 27-inch pits but none from the pits of 22, 23, 26, 26.5,
and 28 inches. In figure 27 are plotted the flies expected, based on all
the adults in the upper 12 inches of soil in all unpacked pits. Suffi-
cient numbers were found at these levels to permit utilization in this
way. The line of expected occurrence agrees at all points very closely
with the records. This is no doubt due to the fact that the soil was
of uniform consistency throughout all depths, being in no way packed.
At the bottom of the pits there were 26 dead flies among the fruit
itself. These have been disregarded since they were not able to move
upward at all. The line may be used to determine the numbers that
might be expected out of a specific population at any level. For ex-
ample, from the line one would expect out of 10,000, the numbers given
in the following tabulation:

Depth in inches:	Adults expected
13	427
16	192
19	93
22	47
25	25
28	13
30	9

In discussing their results, Plummer and Stone pointed out that
one larva traveled upward 22 inches before pupating and that in some
instances adults made their way through 20 inches of soil, and that
if the distance traveled by both stages is taken into consideration,
it would indicate the possibility of emergence through 42 inches. It
is interesting, therefore, to check the curve in figure 27 at 42 inches,
derived as it is from the distribution upward of all adults. A pos-
sibility of emergence at 42 inches is shown.

The diagram may also be projected on the lower line. If this is
extended to represent a depth of 0.1 inch of soil, the indicated effect
from that depth is practically zero. Obviously that depth of soil
would have practically no effect on mortality.

It will be noted that the order of occurrence changes at about 3
inches. The reason for this is not known, but it may possibly indicate
that adults in nature would never be forced to struggle against depths
approaching 3 inches. They may be found in nature at one-half inch
and occasionally under favorable circumstances up to 2 inches.

The discussion and figures that have been here given in regard to
unpacked soil emphasize the importance of burying infested fruit to
adequate depth and thoroughly packing the soil over it. It is proba-
ble, on the other hand, that these experiments represent the most
favorable conditions, since large quantities of soft, moist fruit would
probably produce a certain mortality from the fermentation that
would set in.

The data from the packed pits have been treated in the same way,
and the line has been drawn from the encircled dots. It will be seen

at once that these do not fall regularly as did those for the unpacked
series. Packing does not have the same effect throughout the pit. The
upper layers become solid. The effect on the lower layers is small.
It will be seen that the distribution at 5, 6, and 7 inches is bunched.
At 7 inches a new order of expected occurrence begins and it is as-
sumed that the packing may be responsible for this. It is safest,
however, to judge from the line of the lower occurrences. If this is
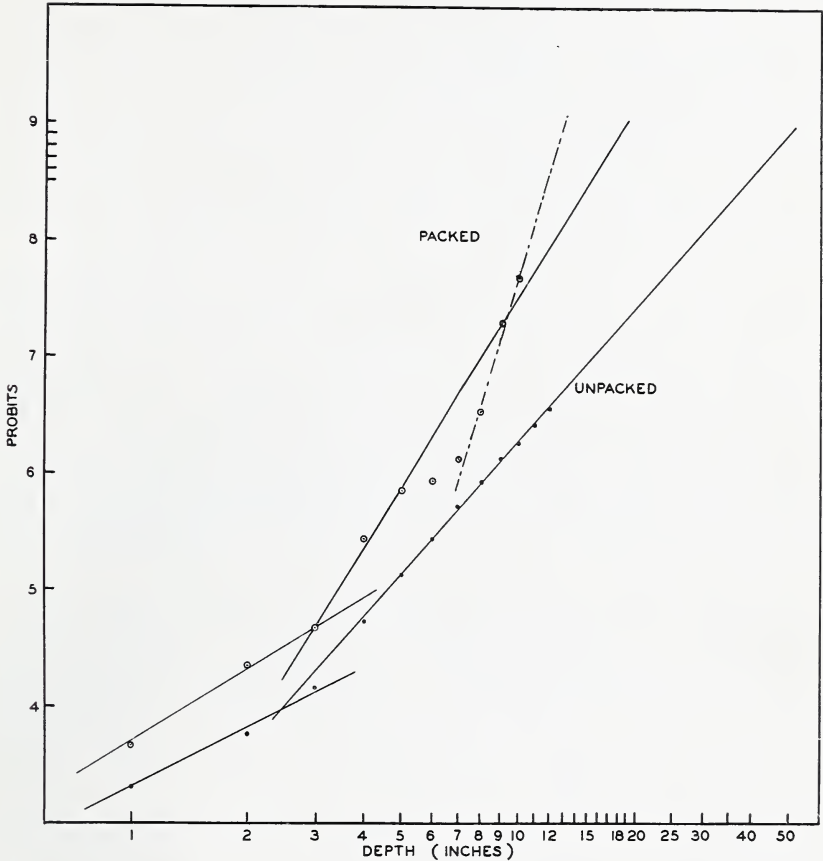
FIGURE 27.—Occurrence of adults of *Anastrepha ludens* at different levels in
packed and unpacked pits containing infested mangoes. The broken line indi-
cates the new order of occurrence as a result of packing. (Data from Plummer
and Stone (*35*).)

read at 18 inches, it is seen to correspond with the line from the
unpacked series at 48 inches; it seems sufficiently certain, therefore,
that 18 inches of carefully packed soil would assure mortality of all
adults under practical methods of disposal.

In grove sanitation under infestation conditions, it is advisable to
dispose of fallen fruit very promptly, since larvae emerge and enter
the ground soon after the fruit falls. In Santa Engracia it was the

custom of the grove manager to pick up fallen fruit daily as far as possible. A case has been reported of one hacienda where the early infested grapefruit were buried, but not to a sufficient depth. Subsequently very large populations of newly emerged flies were trapped in this property. In controlling known infestations proper grove sanitation is of major importance.

PARASITES AND PREDATORS

Parasites play a considerable part in reducing the population of certain fruitflies, and a number of species work on *Anastrepha ludens*. The most common is *Opius crawfordi* Vier. This small ichneumonoid lays its eggs in the larvae with the result that parasites rather than flies emerge from the puparia. As early as September 1900 De la Barreda (*21, p. 24*) discovered this parasite in Cuernavaca in large numbers and gave an account of its attacks on *A. ludens* and of the possibility of its utilization. He referred to it under the name of *Braconus*, n. sp.

Considerable information on *Opius crawfordi* has been obtained from the general rearing work on the flies, and in this way the effect of the species in depressing populations of *Anastrepha ludens* has been observed. Unfortunately the percentage of parasitization is relatively low owing to the difficulty experienced by the female in reaching the larvae embedded deep in fruit such as citrus. Were *A. ludens* confined to fruit with a very small amount of flesh, it is probable that *O. crawfordi* might be a factor of commercial importance. There are as yet no data indicating its precise influence on the populations developed in *Sargentia*, but the rearings from that fruit show that in some cases at least considerable parasitization takes place.

Studies made by Kapp and Darby [88] and by Kapp [89] show that the parasite is influenced by humidity and by temperature, the temperature factors at both extremes having a greater effect on the developing parasite than on the developing fly. No adult parasites were obtained below a temperature of 58.1° F., whereas adults of *Anastrepha ludens* emerged at considerably lower temperatures. At the other extreme no parasites emerged at temperatures above 84.4°, while *A. ludens* adults emerged at higher temperatures.

The numbers on which the mortality for the parasite is based are not large, the percentage figures for *Anastrepha ludens* being backed by much higher numbers. This would probably operate to extend the survival points for *A. ludens* relatively farther in both directions than those for *Opius*, and the difference shown might be less striking with equal numbers.

The relation of humidity to survival of the parasite appears evident in figure 28, which shows a longer duration of life as the relative humidity increased. The parasites were maintained in cages in the laboratory under humidity conditions normally varying there during the change from the dry season to the rainy season. In reading these curves, however, it should be borne in mind that No. III is based on 50 insects, No. II on 40, and No. I on 21.

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[88] See manuscript report 20, p. 153.
[89] See manuscript report 22, p. 153.

In the field percentage of parasitization increases from May to August according to Kapp's data, reaching a peak of about 20 percent or in some years much higher. From February to April it is very low. This situation Kapp interprets as a reflection of humidity. A similar idea is expressed by Darby and Kapp (*14, p. 18*) as follows:

> It might possibly be thought that the abundance of parasites is controlled by the number of *Anastrepha* larvae, and this in turn by the quantity of fruit. Such, however, is not the case.

This statement appears inadequate. It is obvious that in any environment of a normal nature, i. e., where a species thrives, no one factor is an all-controlling one; but sequence, suitability, and abundance of hosts constitute one of the important problems in estimating the fitness of any environment for fruitflies. That host abundance is an important factor in influencing the number of larvae of *Anastrepha ludens* is evident from a comparison of the
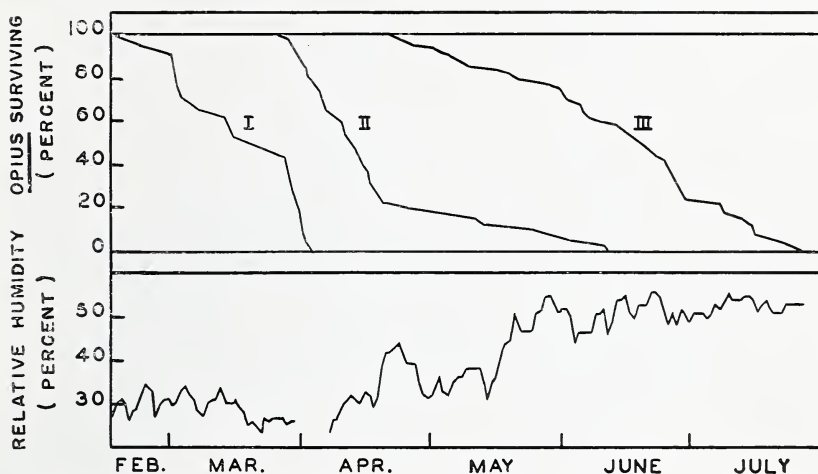
FIGURE 28.—Relation of humidity to survival of *Opius crawfordi*. (After Darby and Kapp (*14*).)

situation in Santa Engracia with that in Cuernavaca. In Santa Engracia there are two abundant alternate hosts, *Sargentia* and citrus, and two large peaks of larval population in them, a fact reflected in the adult population (fig. 11). In Cuernavaca there is only one abundant host, the mango, and one peak in larval population, also reflected in adult population (fig. 10).

In the senior author's opinion the factors which control the abundance of *Anastrepha ludens* are the following: (1) The temperature factor—range and duration of suitable temperatures; (2) the host factor—sequence, characteristics, and abundance of hosts; (3) the humidity factor—extent and distribution of rainfall and of atmospheric humidity; (4) the pathological factor—parasitization by other organisms such as insects, fungi, and bacteria, mutilation or destruction by predatory forms, abnormal physiology (such as derangement of reproductive or metabolic functions); (5) the shelter factor—the availability of cover for adult dispersion, the

character of soil for pupation, etc.; and (6) the adaptation factor—the ability of the species to become adjusted to new conditions. Some data have been gathered on all these factors, but these data only emphasize the complexity of the interactions, the magnitude of the analytical problem, and the necessity of considering that problem as a whole. So far as analysis has gone, the host factor is the most important in its influence on abundance in any suitable environment. This factor, a purely local one, shows the danger in making regional estimates on climatic factors and in adopting a single-factor assumption.

With *Opius crawfordi*, as with *Anastrepha ludens*, it seems obvious that host abundance is an important factor in the abundance of the parasite. The parasite population is the secondary one. That the percentage of parasitization increases as the host population increases would indicate that the number of *Anastrepha* larvae is a definite factor in the number of parasites. When the number of larvae falls with the close of the mango crop, the percentage of parasitization also falls. Of course other factors also enter here, such as the lack of access to larvae in sweet limes, perhaps the principal carry-over fruit in Cuernavaca. It is worthy of note that the diagram showing percentage of parasitization throughout the year which Darby and Kapp (*14, p. 18*) present gives 3 months in which they recorded no parasites. These 3 months are filled in with the words " fruit scarce," an admission that disagrees with their statement previously quoted. These 3 months are September, October, and November. Yet their diagram for rainfall shows abundant rain in September and October, that in October to be approximately equal to that in May, and that in September almost equal to that in June, July, and August.

The fact that parasitization in mangoes reaches some proportions before the crop disappears, led to the belief that under some circumstances *Opius crawfordi* might prove of considerable importance as a parasite of related species of fruitflies. Stone therefore shipped a total of 8,160 living adults to the laboratories in Hawaii and Puerto Rico.

While *Opius crawfordi* is the parasite found attacking *Anastrepha ludens* in largest numbers, several other species which attack the larva or pupa have been reared, although no studies have been made of these because of their relative scarcity. The species involved will be briefly mentioned. In all cases determinations have been made by the Division of Insect Identification of the Bureau of Entomology and Plant Quarantine of the United States Department of Agriculture.

In addition to *Opius crawfordi*, McPhail and Bliss (*29, p. 22*) reared *Galesus* sp., *Eucoila* sp., and *Anthrax scylla* O. S. *Galesus* sp. was reared only from field-collected puparia, never from field-collected larvae, and presumably is therefore a parasite of the pupa. Since *Eucoila* sp. was reared from both, it probably, like *O. crawfordi*, parasitizes the larva. *A. scylla* was obtained from field-collected puparia.

In Hacienda Santa Engracia, McPhail [90] reared several parasites from *Anastrepha ludens* found feeding in *Sargentia*. *Opius crawfordi*, common in the Cuernavaca region, also attacks *A. ludens* in this wild fruit. It is possible, therefore, that this was the original

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[90] See manuscript report 67, p. 154.

association existing between host and parasite. Two other species also occurred, *O. cereus* Gahan and a new species of *Opius*. No detailed studies were made on the influence of these other species on *A. ludens* in its natural habitat. The same undescribed species of *Eucoila* found by McPhail and Bliss in Cuernavaca was reared also by McPhail on the hacienda.

Other parasites emerged from lots of miscellaneous material from infested *Sargentia*; two new species of *Phanerotoma*, a new species of *Lissonota*, and one of the genus *Urosigalphus*. It is probable, however, that these forms were parasitic on other insects present with *Anastrepha ludens*.

McPhail reared a new species of *Opius* in the *crawfordi* group from puparia of *Toxotrypana* sp. from Santa Engracia.

Skwarra undertook a special study of the species and conditions which depress the populations of *Anastrepha ludens* in the environments she visited. In these studies she collected a large number of specimens found associated with *A. ludens*, especially ants, which she found commonly attacking the larvae. She has not yet completed the classification and evaluation of all this material, and no attempt therefore will be made to summarize the conclusions that may follow from her analysis of it.

The only other study on predators that has been conducted is a preliminary one by Stone [91] on predatory forms attacking larvae in Cuernavaca.

A number of species were observed, but the commonest and most important was a staphylinid, *Xenopygus analis* (Er.). Insectary studies with this species showed that as many as 242 larvae were apparently destroyed by a single staphylinid, although 28 larvae died in the control group. Averages for individual beetles per day were from 1.17 to 2 larvae destroyed. The greatest longevity for *X. analis* was found on fruit and water rather than on larvae and water, 178 days against 137 days, but longevity was more consistent on larvae and water. On water alone one specimen lived 83 days.

During the study it was found that the beetles made circular holes in the fruit and through these entered in search of fruitfly larvae. Infested mangoes given the beetles were in this way cleared of all larvae, although the predators did not enter mangoes as readily as they did guavas. One beetle entered nine whole guavas and one broken one. Sometimes two or three entrance holes were made in a fruit. The beetles located and destroyed most of the larvae in these guavas. Figure 29 shows the appearance of guavas after beetles have entered them. One is a fresh fruit, and the other a dried one.

No study has been attempted of the diseases of the larvae, as distinct from insect parasitization. Diseases, probably of parasitic origin, no doubt occur, as larvae are not infrequently found which are partly discolored (fig. 13, *A*). Larvae often die from various causes, such as fermentation of the fruit, but such larvae remain a natural color. The discolored larvae presumed to be infected remain alive, and it is only after much of the body has become discolored that they ultimately die. As the numbers of such larvae found are very small, and the condition appears, therefore, not to be an economic factor of

importance, no attempt has been made to study the pathology to to determine whether the condition is due to infection or to some deranged physiological condition.
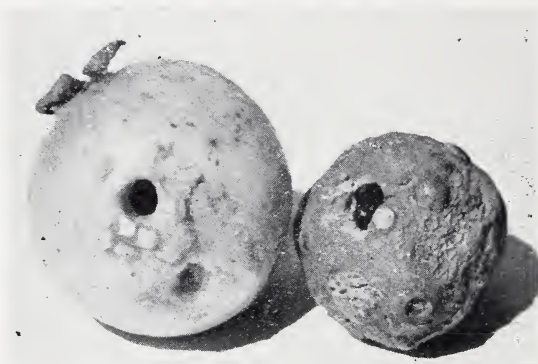

FIGURE 29.—Guavas showing holes made by predatory beetles searching for fruitfly larvae.

STUDIES ON THE PUPAE

LOCATION OF THE PUPARIUM

The puparia, which are illustrated in figure 30, are usually formed in the soil which the larvae enter after leaving the fallen fruit or after dropping from infested fruit still on the tree.

Darby and Kapp [92] (14) acidulated soil in Petri dishes with hydrochloric acid, one series in the center and one series on the periphery, so as to obtain a pH gradient. They found that the larvae of *Anastrepha ludens* selected a concentration of pH 7 or above and that if pupation occurred at pH 6 or below, it was delayed and abnormality resulted. These authors based this test on measurements of the hydrogen-ion concentration of soil surrounding guava fruits where *A. striata* larvae had pupated. Here they found it from pH 6.8 to 7.3, as compared with pH 4.6 to 4.8 beneath the fruit. In regard to *A. ludens* they state (14):

* * * Information on the effect that the hydrogen-ion concentration has on the immature stages of the fly suggests that this factor affects the distribution and relative abundance of the fly in Mexico both as to location and host fruit.

Unfortunately for their assumption, infestation has now advanced, as it had formerly advanced elsewhere, to regions they considered more or less protected by this factor.

The conception of Darby and Kapp that larvae migrate to and pupate in definite zones extending outward from the fallen fruit, depending on a pH gradient in the soil produced by the decaying fruit, is discounted by Skwarra [93] from observations made on larvae leaving fruit and seeking locations for pupation. She found that

[92] See manuscript report 15, p. 152.
[93] See manuscript report 24, p. 153.

on an average the larvae move 10 to 12 cm. per minute, and that they move in a haphazard way, wandering about and frequently returning to the starting point. If in this wandering the larva encounters a small lump of soil, it immediately burrows at the point of contact between the lump and the remaining surface. Under leaves she found the larvae pupating without burrowing, and in places where there was a heavy mulch pupation took place in the mulch. In sod she found pupation on the soil surface with no attempt to burrow, and in 1927 Baker found that he could induce pupation in otherwise restless larvae in glass containers by covering them with grass. Skwarra found that on hard ground larvae pupate immediately beneath fallen, decaying fruit between the fruit and the ground, and that if the fruit has lain for some time, so that the soil beneath it has become moist, whereas surrounding soil is dryer, the larvae will bur-
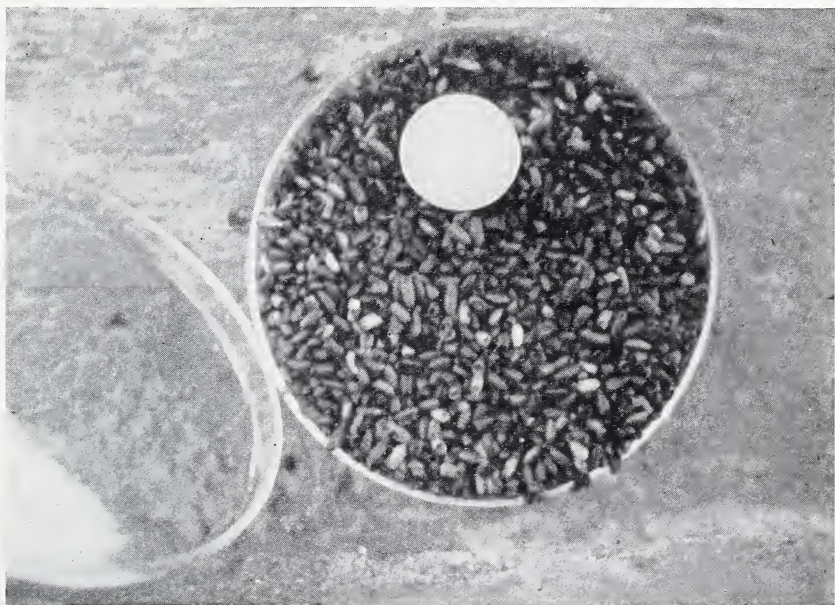
FIGURE 30.—Puparia of *Anastrepha ludens*. There are openings in some of the puparia from which flies have emerged.

row directly beneath the fruit and then pupate. As a rule the puparia are found about half an inch below the soil surface. The depth, however, depends largely on the nature of the soil. The exact stimulus that causes burrowing which precedes puparium formation is not known.

Plummer [94] in 1931 conducted several tests the results of which also seem at variance with the conception of Darby and Kapp. Soil was reduced from the existing pH 7.01 to pH 4.2 by the use of aluminum sulfate. The treated soil was arranged in a tray 93 inches long and 12 inches wide, the soil being 1.5 inches deep. In a 6-inch space at one end of the tray 195 full-grown larvae of *Anastrepha ludens* were

[94] See manuscript report 68, p. 154.

liberated. Later examination showed an arrangement of puparia and larvae as follows:

Soil location (inches):

	Individuals found
1 to 6 (beginning at point of liberation on soil)	132 well-formed puparia, 2 poorly formed puparia, 4 living larvae, and 16 dead larvae.
6 to 12	21 well-formed puparia and 1 dead larva.
12 to 18	8 well-formed puparia.
18 to 24	2 well-formed puparia.
24 to 30	2 well-formed puparia and 1 poorly formed puparium.
30 to 36	1 well-formed puparium, 1 poorly formed puparium, and 1 living larva.
36 to 42	1 well-formed puparium.
42 to 93	None.

Twenty-five larvae in normal soil were retained as a control. These gave 17 well-formed puparia and 8 dead larvae.

The experiment was supplemented with another in which a soil of pH 5.87 was obtained by treatment with ammonium sulfate. The results in this test were as follows:

Soil location (inches):

	Individuals found
1 to 6	160 well-formed puparia, 5 poorly formed puparia, and 14 dead larvae.
6 to 12	29 well-formed puparia and 2 dead larvae.
12 to 18	7 well-formed puparia.
18 to 24	5 well-formed puparia.
24 to 30	1 well-formed puparium.
30 to 36	None.
36 to 42	1 well-formed puparium.
42 to 93	None.

The control contained 21 well-formed puparia, 1 poorly formed one, and 3 dead larvae. These experiments appear to indicate that any abnormality resulting from pupation in acid soils is at least not marked and hardly sufficient to account for differences in distribution of the insect.

Length of Time Spent in Puparium

The length of time spent by the insect within the puparium is important from the practical viewpoint because not only does it determine in part the number of generations that may be produced but if the insect were able to tide over adverse conditions in this way it could survive where it might otherwise perish. So far as studies have revealed, there is no hibernation or hold-over as puparia from one year to the next, as is found with many insects. Duration of the puparial period is very largely a function of temperature.

The earliest observations on the duration within the puparium are apparently those made in Washington, D. C., on material received from Townsend in 1897 (22, pp. 544, 545), although the exact duration is not given. Johnson (24, p. 55) obtained an adult after 38 days, and he reported that Bruner had obtained one in about 41 days. It is perhaps worthy of note that in the room where Bruner kept his breeding cages the mercury fell below freezing on several occasions. Herrera and his associates (21, p. 14) found the duration within the puparium to range from 17 to 25 days and from 30 to 46 days. Crawford (8, p. 179) in the Tampico region recorded 25 to 30

days in winter and 20 to 25 days in summer. McPhail and Bliss (*29, p. 13*) found the time in the field in Cuernavaca to be directly dependent on temperature, although their figures for 1928 and for 1929 gave somewhat different curves, as shown in figure 31. The daily temperature range in the 2 years differed by 13.2 Fahrenheit degrees, but this alone does not account for the difference, and an error in thermograph calibration was assumed.

Kapp and Darby [95] undertook a complete laboratory study of the time spent within the puparium in relation to temperature, using incubators and close temperature intervals. They obtained the duration as from 12 days at 87.8° to 107 days at 53.4° F.
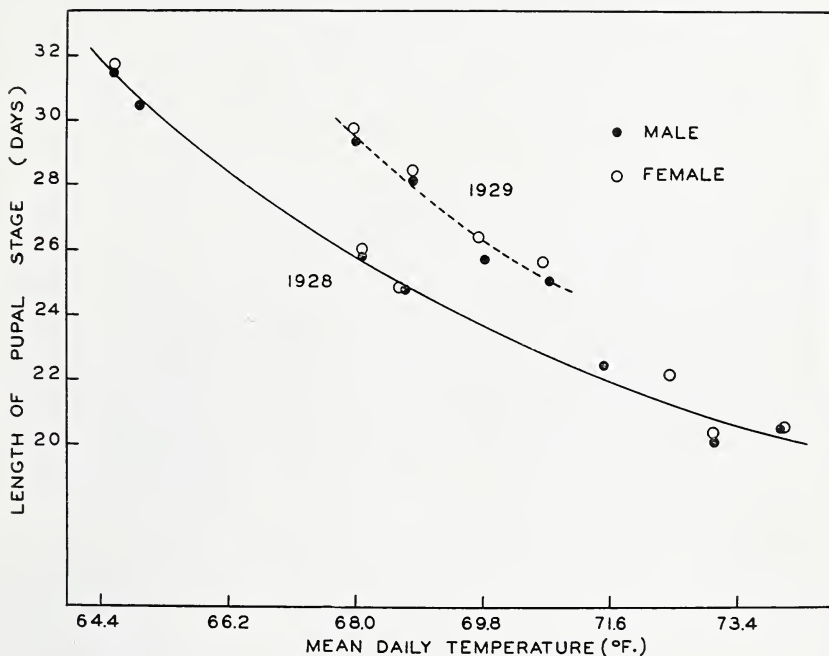
FIGURE 31.—Time spent by *Anastrepha ludens* within the puparium as influenced by temperature. (After McPhail and Bliss (*29*).)

From these data and a record of the soil temperatures in any locality, granting adequate humidity, it is possible to estimate the length of time the insect will remain in the soil, and predictions made on these records have been fulfilled. In their work Kapp and Darby used a 24-hour period, midnight to midnight, in establishing age so that in 1 day's puparia there was included the variation resulting from puparia formation throughout the 24-hour period. This procedure was fully satisfactory for obtaining the duration records needed, since it was known that there was some variation in emergence. At the time it was not realized that, the more prolonged the duration of the pupal period, the more prolonged would be the period during which flies emerge.

In figure 32 is plotted the minimum duration in relation to tem-

perature on the assumption that this represents the most vigorous individual. As can be seen from the figure, the direct relationship holds closely between 16° and 29° C. (60.8° and 84.2° F.). It is a fair assumption, therefore. that puparia of *Anastrepha ludens* will have a satisfactory development in soils remaining between 60° and 85° F. Soils remaining at 90° would not permit their survival, and in soils remaining as low as 50° no development would occur.

Soil temperatures a short distance below the surface are very even compared with air temperatures, and thermograph records from soils in Weslaco and Brownsville, Tex., show that the soils of
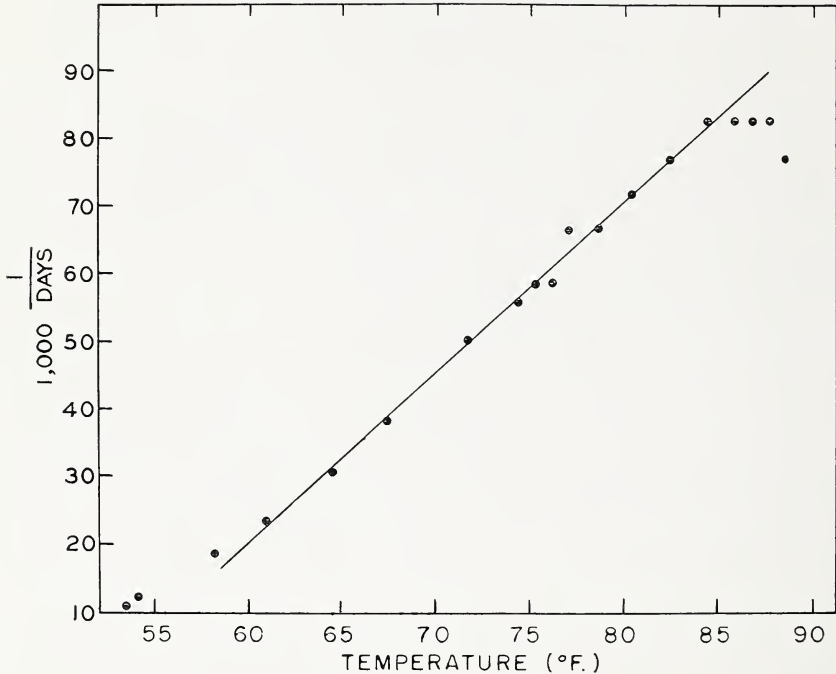
FIGURE 32.—Relation between temperature and minimum length of time spent by *Anastrepha ludens* within the puparium. (Data from Darby and Kapp (*14*).)

the Rio Grande Valley remain during most of the time within the range given as that of normal development. During protracted cold waves the records show soils at about the lower range of this normal development but not at destructive temperatures. On the other hand, soil-temperature records for August show periods in which the temperature has remained above that permitting survival. These records are taken in the usual manner, and it is very probable that under trees in the dense shade soil temperatures above those supportable by the puparia would not be reached or maintained. Nevertheless the records indicate that soil temperatures in open, unshaded areas would be too high for survival. In Texas there are certain wild fruits which grow on very low, open bushes on sandy ridges. Such fruits at first glance would appear ideal for infesta-

tion, but adults ordinarily do not frequent hot open areas, and even if the fruits became infested it is probable that summer soil temperatures in such environments would destroy the puparia.

As represented by figure 32, the shortest duration within the puparium under high temperatures (31° C. or 87.8° F.) was 12 days. A temperature of 90° F. would have to prevail in the soil, therefore, for a considerable period of days to cause destruction. According to the records, however, this may occur. Temperature experienced would of course depend on the depth to which the larvae had penetrated.

Information on the possible influence of larval food on duration within the puparium was not obtainable from the data by Kapp and Darby, since all the larvae from which they obtained their puparia were from mango. It remained for Stone [96] to check this point in his work at 77° F. with different fruits. His results appear in table 2. An influence of the character of food on length of larval life is well shown, but an influence on duration within the puparium is not so distinctly evident.

A preliminary attempt was made by Baker [97] to determine the influence of time of emergence as a life process on duration of life within the puparium. As with Stone's work, first emergence from each lot in the series was adopted as the measure. Puparia were held at 82.4° F. Those forming each hour between 1 a. m. and 8 a. m. were segregated and maintained under as nearly uniform conditions as possible. The results, while not conclusive, appear suggestive, as the data in table 4 show. In work of this kind the selection of first emergence in the different lots gives a more uniform result, since it is based on vigorous and normal individuals. Last emergence reflects the weakest individuals and is usually very irregular. The mean is influenced by these weak specimens.

TABLE 4.—*Influence of emergence, as a life process, on duration of life of Anastrepha ludens within the puparium*

Hour by which puparia were formed (a. m.)	Duration of life within puparium as measured by first emergence in each group of puparia		Hour by which puparia were formed (a. m.)	Duration of life within puparium as measured by first emergence in each group of puparia	
	Days	*Hours*		*Days*	*Hours*
2	14	8	6	14	3
3	14	7	7	14	3
4	14	6	8	14	0
5	14	4			

These various studies concerned the relative duration of life within the puparium at given temperatures. The question of the distribution of duration in a given field population is also of interest. Figure 33 is a smoothed curve for the life expectancy within the puparium on the basis of a field population of something over 1.200. Granted a temperature range in which the population will normally develop, expectancies of time to emergence are about what would be anticipated.

[96] See manuscript report 48. p. 153.
[97] See manuscript report 64. p. 154.

Effects of Moisture on the Puparium

Rearing of enormous numbers of adults for experimental work has shown that moisture conditions are an important factor in the mortality of the stages passed within the puparium. Among the workers at the laboratory this was first pointed out by McPhail and Bliss (*29, pp. 13, 14*), who found that the soil moisture had little effect
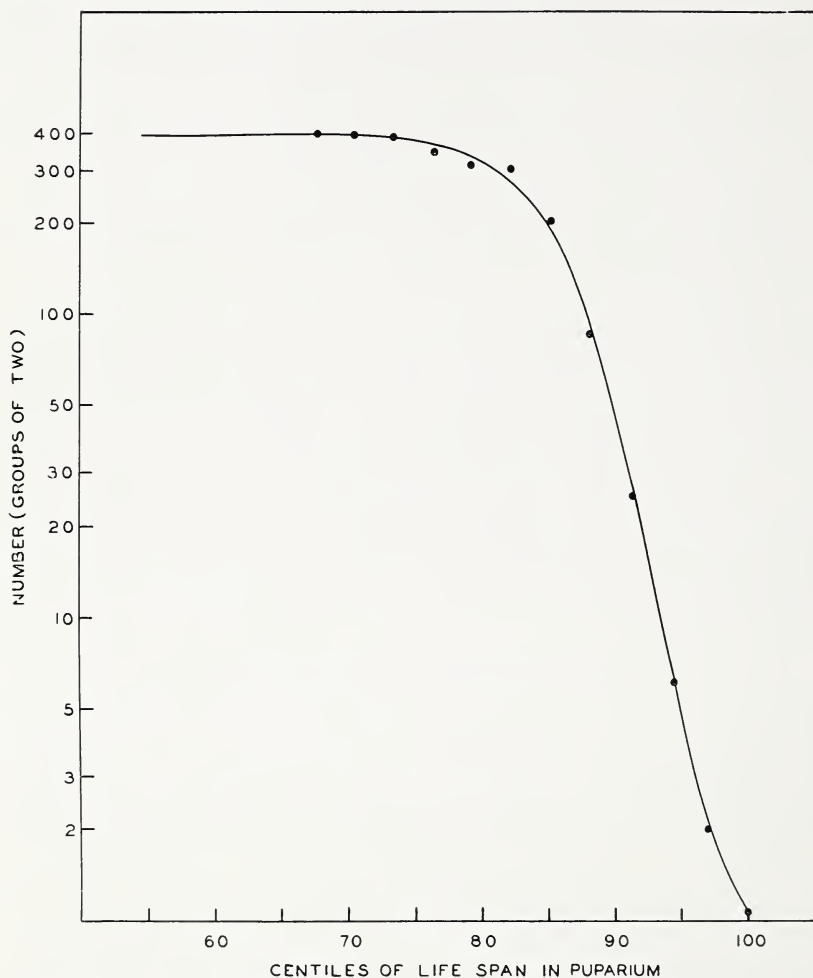
Figure 33.—Expectancy of life of *Anastrepha ludens* within the puparium. (Data from McPhail and Bliss (*29*).)

on the duration of life within the puparium but a definite effect on mortality, and that this effect was mostly operative during the first few days of life in the puparium. Probably, therefore, the greatest effect is on the prepupae. Darby and Kapp [98] compared moist soil with dry, obtaining 69.3 percent emergence with the former and only 4.6 percent with the latter.

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[98] See manuscript report 15, p. 152.

The influence of moisture on body weight in connection with emergence was studied by Darby and McPhail.[99]   Their results are shown in figure 34.   The effect of desiccation is at once apparent.

This question of the mortality of puparia during very dry seasons or under very dry conditions may have a bearing on the magnitude of adult populations in different years or in limited areas.   Presumably where trees are large, formation of puparia in the shade beneath them would meet with favorable conditions even in dry weather, but this may not always be the case.

The question of survival of puparia under conditions of flooding was studied by Baker.[1]   Records had shown that fruits would often float for long periods, and not only the survival of puparia under
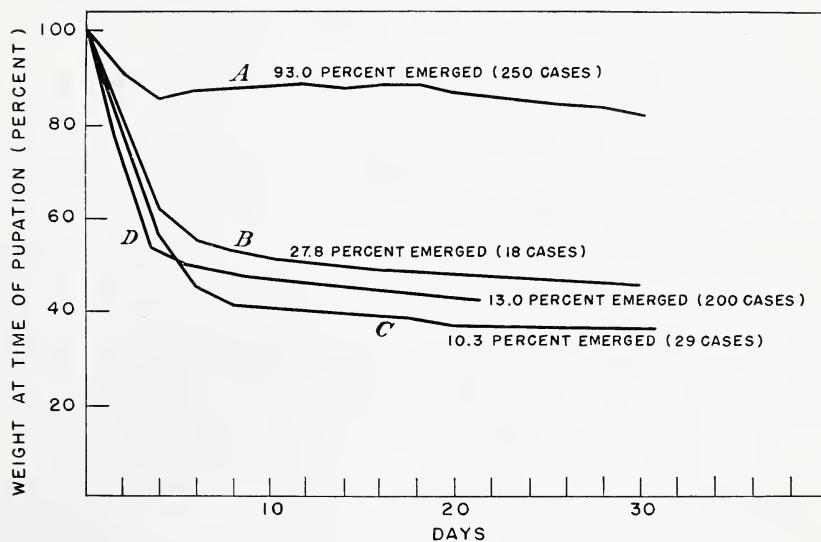
Figure 34.—Effect of moisture on weight of puparia of *Anastrepha ludens* and on emergence: *A*, Puparia kept on wet cotton; *B*, kept in dry Petri dish; *C*, kept in dry Petri dish; *D*, kept dry and desiccated at intervals.   (After Darby and McPhail, No. 17 in Manuscript Reports Cited.)

flood conditions but possible transfer of infestation appeared involved. Puparia of *Anastrepha striata* were therefore placed in water, removed after various intervals, and held for emergence.   Some puparia sank at once whereas others floated for different time periods.   Puparia that floated 4 days before sinking gave 8 percent emergence when removed at once.   Those that continued to float longer than 4 days gave no survival.   Those puparia that sank at once and were immediately removed gave a higher emergence than was obtained in the control.   It appears, therefore, that floating puparia are less hazardous than those that do not float, although a flotation of 4 days still permits some emergence.   Obviously puparia could be carried a considerable distance in that time.

[99] See manuscript report 17, p. 153.
[1] See manuscript report 35, p. 153.

TEMPERATURES FATAL TO STAGES IN THE PUPARIUM

Darby [2] and Darby and Kapp (*13*) studied the mortality exhibited by puparia of different ages held at high and low temperatures beyond the points of possible survival. Recently formed puparia were exposed to temperatures of 102.2°, 103.1°, and 104.9° F. for various lengths of time (fig. 35). Older puparia in which pupa formation had been completed for some time were more hardy, being unaffected by temperatures and exposures that produced a complete kill of the stages in recently formed puparia. It was found with these older, more hardy puparia that at 103.1° more than 20 hours were required for a 100-percent kill, and at 104.9° about 13 hours.
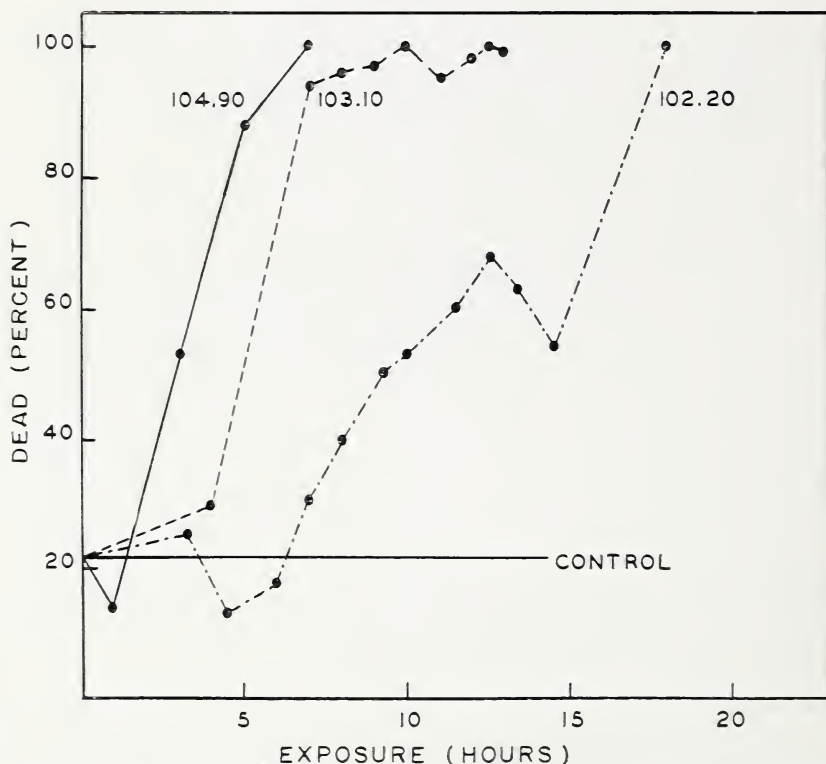
FIGURE 35.—Mortality of pupae of *Anastrepha ludens* at high temperatures. (After Darby and Kapp (*13*).)

Darby and Kapp (*13*) confined their attention, as far as low temperatures are concerned, to 39.56° and 49.46° F. and developed mortality data with puparia of different ages. With recently formed puparia complete mortality was obtained at 39.56° in 15 days whereas at 49.46° complete mortality was not obtained for 30 or more days.

Puparia were held at intervals of 2 days for periods up to 10 days at 77° F. previous to exposure to 39.56° F. The effects of exposure to this temperature are shown in figure 36. The striking points in these

[2] See manuscript report 25, p. 153.
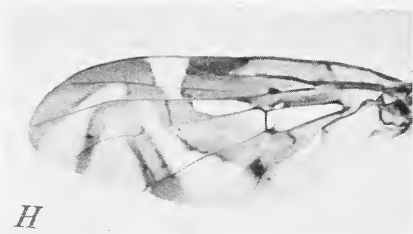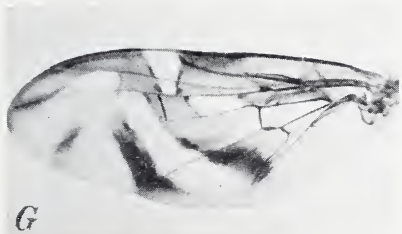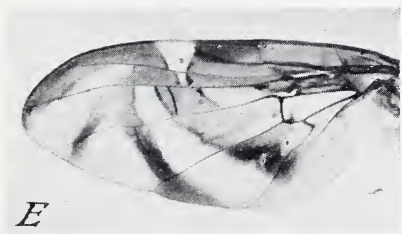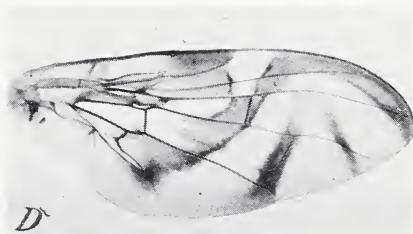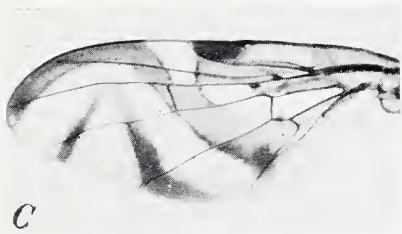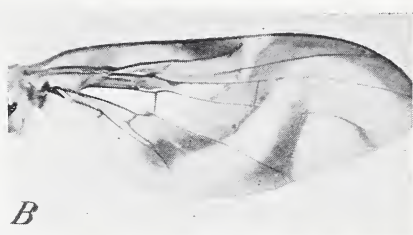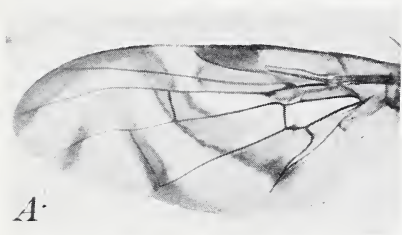
WINGS OF FRUITFLIES

A, *Anastrepha ludens* with open costal markings; B, *A. striata;* C, *A. distincta;* D, *A. ludens* with closed costal markings; E, Mexican *A. mombinpraeoptans* from Cordoba; F, *A. mombinpraeoptans* from Puerto Rico; G, Mexican *A. mombinpraeoptans* from Morelos; H, *Lucumaphila sagittata.*

results are (1) the greater resistance to low temperatures where newly-formed puparia are concerned in comparison with those formed 2 days previously and (2) the marked resistance shown by puparia of 4 days as compared with newly-formed puparia and puparia of 2, 6, 8, and 10 days.

Darby and Kapp add that 4 days at 77° F. is about the time when the change from the fourth larval instar to the pronymph condition takes place within the puparium. They state, however, that their experiment was not critical enough to prove any relationship between resistance and this change.
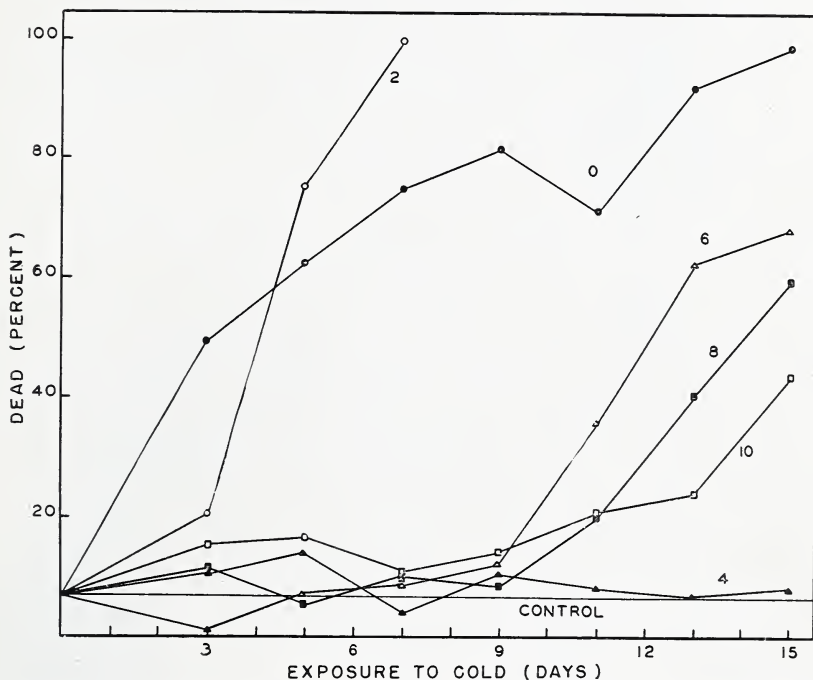
FIGURE 36.—Mortality in puparia of *Anastrepha ludens* when exposed at 39.56° F. Numbers on lines represent age of the pupae expressed in days they had previously been held at 77° F. (After Darby and Kapp (*13*).)

STUDIES ON THE ADULTS

APPEARANCE OF THE ADULTS

The adults are beautifully colored flies about the size of houseflies. The eyes are green. The body is yellowish brown. The thorax, especially in newly emerged flies, has pale longitudinal markings somewhat lighter than the remaining color. Generally there is a small median spot of dark brown on the posterior part of the mesothorax. The wings are banded with yellow and brown. The details of the wing markings may be seen in plate 7, *A* and *D*. The inverted **V** on the lower part of the wing is broken at its tip and is not connected with the main pattern, as it is in certain other closely related fruitflies.

The ovipositor sheath of the female is long and slender. The

tip of the sheath is armed with a large number of strong, recurving teeth, as can be seen in figure 37, *A*. These teeth are located on a membrane which may be withdrawn into the tip of the sheath, and ordinarily they are not visible, as the membrane is usually carried within the sheath. The ovipositor itself is long, bladelike, and armed at the tip with fine serrations and numerous sensoria (fig. 37, *C*). It is heavily sclerotized, thus permitting puncture of the skin of fruits. The opening of the ovipositor is centrally located close to the serrated portion and is armed with a setose membrane.
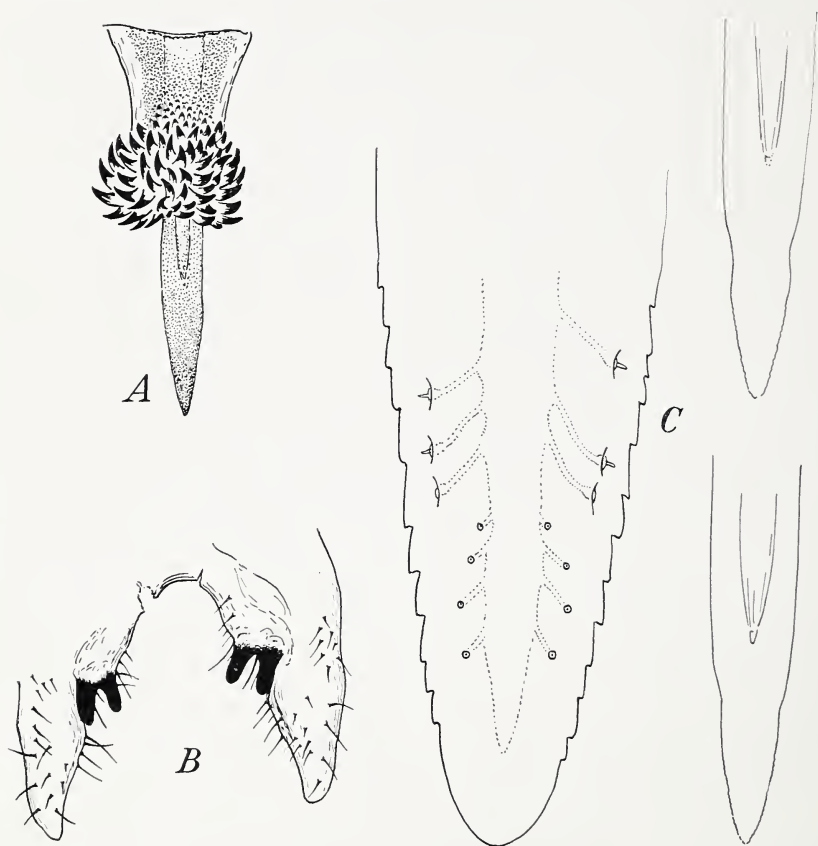
FIGURE 37.—Reproductive organs of *Anastrepha ludens:* *A*, Tip of ovipositor sheath, showing recurving teeth; *B*, claspers of the male; *C*, tip of ovipositor, showing sensoria and marginal teeth.

In the study of large numbers of ovipositors of *Anastrepha ludens* it has been found that two types exist. They differ in the distance between the ovipositor opening and its tip, as shown in figure 38. The form with the shorter distance is rather consistent in mango material from Cuernavaca and in *Sargentia* material from Santa Engracia. The one with the longer distance has been found in trap material from Santa Engracia and also in material reared from grapefruit

there. Grapefruit material shows several types including the two extremes. The question of possible races of *A. ludens*, as reflected by such differences, has not as yet been fully studied. It should not be forgotten, when considering the possibility of races, that mangoes are relatively free from attack in the north although this fact may be due only to the presence of *Sargentia* there, as a more normal summer host than mango.

Individuals differ in size, depending on the nourishment the larvae have received and the resulting size of the puparia. The length of the ovipositor sheath of the female especially is variable, and this variability does not always correspond to the size of the individual.

Stone [3] made a study of this variability, plotting measurements of the ovipositor sheaths of 200 females captured in Cuernavaca and the sheaths of 100 females reared in the laboratory in Mexico City. It will be seen (fig. 39) that the laboratory-reared flies were smaller than

FIGURE 38.—Variation shown in the ovipositors of females of *Anastrepha ludens*.

those taken in the field, a fact which probably indicates more advantageous conditions in nature. On the other hand, in laboratory populations practically all specimens are conserved, and a field catch, therefore, may represent a much more selected population. This particular laboratory population, moreover, was reared from larvae taken from fruit before they had emerged naturally.

The male claspers (fig. 37, *B*) are elongate, triangular, and each possesses two heavy, rounded teeth near the middle which are located in a differentiated area. These teeth serve to hold the ovipositor during coition.

Stone [4] also found that flies reared from peppers are definitely darker than those from citrus. Populations from citrus gradually darkened, however, over a period of 2 months, and thereafter no difference in color could be noted.

[3] See manuscript report 47, p. 153.
[4] See manuscript report 48, p. 153.

Baker [5] has reported a curious abnormality among certain females in Cuernavaca, in that the ovipositor sheath becomes amputated a short distance from the tip. The abnormality appears first as a small black spot, which gradually encircles the sheath (fig. 40, *A*), the tip of which falls away as shown in figure 40, *B*. The ovipositor itself is not altered, but its tip usually protrudes slightly from the amputated sheath, although it may be extended and withdrawn in the usual way. Otherwise the females appear normal. Stone conducted breeding tests with a series of these "short-tailed" flies, but was unable to obtain offspring.
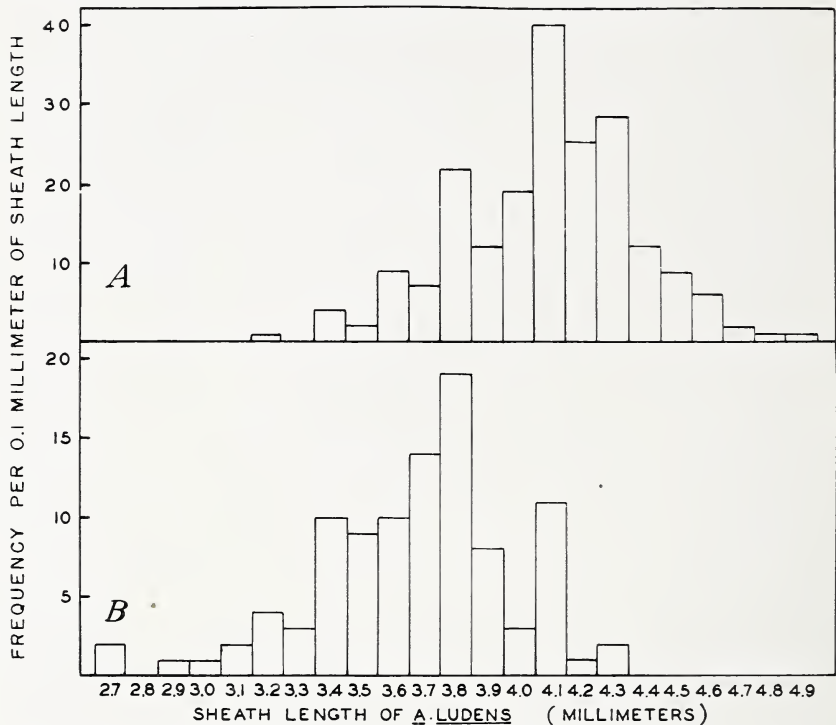
FIGURE 39.—Distribution of ovipositor-sheath lengths in field and laboratory populations of *Anastrepha ludens*: *A*, Data from 200 females trapped in the field; *B*, data from 100 laboratory-reared females. On account of the numbers of flies compared, the ordinate of *B* is shown as twice that of *A*.

Occasionally intersexes are taken in nature, one side of the fly showing the characters of the male, while the other shows those of the female. In these cases there is usually an abnormally formed clasper on one side and a much reduced and distorted ovipositor sheath on the other, the ovipositor itself protruding at an angle.

Sports occur occasionally in the laboratory, showing modification in wing structure, etc., much as has been recorded with *Drosophila*, but no attempt has been made to breed these or to study them from the genetic viewpoint.

[5] See manuscript report 48, p. 153.

Premating Period

The adults emerge from the puparium by distention of the ptilinum. This bladderlike structure on the front of the head also aids them in reaching the surface of the soil. The sexes occur in about equal proportions. McPhail and Bliss (*29, p. 15*) noted a marked diurnal fluctuation in time of emergence, over 95 percent emerging between 6 a. m. and 10 a. m. They accumulated data indicating that exposure to sunlight or higher temperature stimulates emergence, a conclusion that may be compared with the data by Baker from hourly formation of the puparia. Darby and Kapp [6] assembled data indicating that males tend to emerge before females.
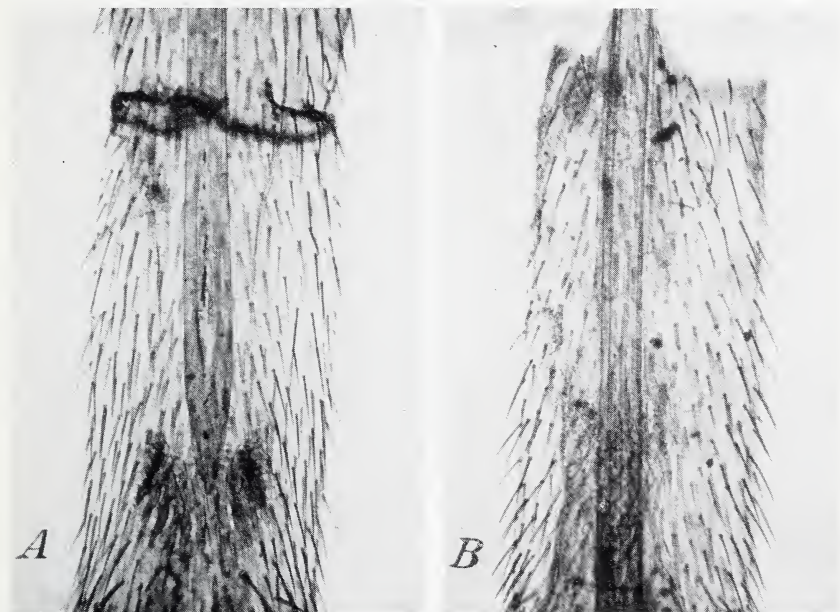
Figure 40.—Amputation in nature of the tip of the ovipositor sheath of *Anastrepha ludens: A*, Girdling nearly completed; *B*, sheath tip amputated.

The flies are not sexually mature when they emerge, if this may be determined by the first mating. The time intervening between emergence and first mating varies with the time of year, and is probably dependent upon temperature. McPhail and Bliss (*29, p. 16*) found it to range from 8 to 34 days, the shortest period being under the highest mean temperatures, while the two longest periods were under the two lowest mean temperatures. As judged from their attempts to mate, the males reach maturity before the females. Unmated females, however, commonly deposit eggs.

Mating and Oviposition

As a rule, mating occurs in the late afternoon or early evening, a fact early recorded by McPhail and Bliss, although mating at different times of the day is commonly observed with laboratory popula-

[6] See manuscript report 15, p. 152.

tions. The act usually requires less than half an hour, although McPhail and Bliss have observed pairs in copula for $3\frac{1}{4}$ hours. The penis of the male is long and ribbonlike, and is ordinarily coiled in the tip of the abdomen. During mating it is inserted through the membranous slit near the extremity of the ovipositor. Certain closely related flies, which have commonly been grouped with the species of *Anastrepha*, do not possess this long coiled penis, although the ovipositors themselves are even more long and slender.

The female usually begins laying soon after the first mating, and oviposition may continue irregularly during much of her subsequent life. It may happen, however, that laying is greatly delayed during cool weather; for example, McPhail and Bliss recorded a preoviposition period of 19 days after first mating. It is worthy of note that when flies first appear in the Rio Grande Valley of Texas in the fall or early winter, as the grapefruit crop is maturing, many of the females do not contain developed eggs, and it is often several weeks before females laden with eggs are captured. This is not surprising in view of the long premating period previously cited.

The number of eggs laid by individual females varies, as does also the distribution of ovipositions over the entire period. McPhail and Bliss have recorded a female that laid 401 eggs. Plummer found females depositing fertile eggs in Cuernavaca after 150 days, and Kapp,[7] in Mexico City, has recorded viable eggs from a female 7 months old, and spermatozoa in all stages of development in the testis of a male 9 months old. However, later studies by Plummer have shown that few eggs are laid by very old females and that only a low percentage of these are viable. Females 7 months old laid a small number, of which approximately 24 percent were viable. Females 9 months old deposited very few eggs, only one of which produced a larva.

The eggs are normally laid through a puncture in the skin of the fruit made by the ovipositor of the female. The punctures can be detected only with difficulty, excepting in fruits from which juice tends to exude from the slightest wound. McPhail and Bliss have shown that, as the season progresses, not only is there an increase in oviposition punctures per female, but there is an increase in the number of eggs that hatch. This is associated with increasing temperature. These facts account for the higher build-up during the latter part of a crop season, as compared with lower infestations during the height of a crop such as citrus. The crops that ripen during the summer season, however, are subject to the maximum oviposition and maximum hatch of larvae.

Under severe conditions citrus fruit may be frozen on the trees, and the question arose as to whether adults would oviposit in such fruit after it had thawed. Stone [8] investigated this point by freezing grapefruit artificially and giving adults access to it. Frost covered all the fruits, and when some were cut open crystals of ice could be scraped from them. When these were thawed, females oviposited in them, although, since frozen fruit rapidly breaks down, it is evidently not a very satisfactory medium for the larvae. Nevertheless, fully matured larvae developed in them.

[7] See manuscript report 21, p. 153.
[8] See manuscript report 52, p. 153.

Santillan, in Herrera et al. (*21, p. 6*), attempted to breed *Anastrepha ludens* in the highlands of Mexico but reported that it did not copulate or puncture fruit there. It is probable that he did not anticipate a suitable preoviposition period, for the laboratory has found no difficulty in breeding the insects and in obtaining large quantities of eggs under the conditions existing in Mexico City.

Effect of Temperature on the Adults

Herrera and assistants (*21, pp. 76, 77*), probably the first to conduct specific experiments, concluded that adults cannot withstand low temperatures. They state from tests that 35.6° F. is the lowest the flies would tolerate.

Skwarra,[9] during a survey of locations in Veracruz, inclined to the view that Coatepec, where she estimated that night temperatures reached around 48° F., would not support *Anastrepha ludens* populations in the winter.

Darby[10] and Darby and Kapp (*13*) exposed adults to various low temperatures for different periods, as shown in table 5. Temperatures used were much below those mentioned by Skwarra. Mortality was not unusual after exposure for a week at a minimum of 35.6° F. and a mean a little above 37.4°. The tendency for mortality to increase rather rapidly on long exposure was nevertheless evident. It should be observed, however, that the maximum temperature in these cases never exceeded 44.6°. In the field the fluctuation is usually much greater, and there would be a period in the middle of the day when flies would become active, whereas in these long laboratory exposures the flies were inactive during the entire time, owing to the low maxima to which they were subjected.

TABLE 5.—*Effect of laboratory exposures to cold on adults of Anastrepha ludens* (After Darby and Kapp (*13*).)

Exposure (days)	Flies used	Temperature						Flies dead
		Mean		Maximum		Minimum		
		° C.	° F.	° C.	° F.	° C.	° F.	
	Number							*Percent*
¾	100	5.03	41.05	6.75	44.15	4.25	39.65	1.0
1	100	5.03	41.05	6.75	44.15	4.25	39.65	1.0
1⅚	100	5.10	41.18	7.00	44.60	4.25	39.65	2.0
2⅙	100	5.49	41.88	7.00	44.60	5.00	41.00	3.0
2 1/12	100	5.61	42.10	8.00	46.40	5.00	41.00	4.0
3	300	4.96	40.93	5.50	41.90	4.00	39.20	3.7
4	100	5.64	42.15	10.00	50.00	2.75	36.95	5.0
4	200	2.98	37.36	4.50	40.10	2.00	35.60	2.5
5	150	5.06	41.11	10.00	50.00	2.75	36.95	8.0
6	100	3.03	37.45	5.00	41.00	2.00	35.60	9.0
8	100	3.09	37.56	5.00	41.00	1.50	34.70	35.0
10	100	3.25	37.85	5.00	41.00	1.50	34.70	67.0
12	100	3.08	37.54	7.00	44.60	2.00	35.60	78.0
13⅓	100	3.23	37.81	7.00	44.60	2.00	35.60	89.0
15	100	3.36	38.05	7.00	44.60	2.00	35.60	98.0

The tests by Darby and Kapp were conducted in the laboratory, but Stone[11] conducted tests outdoors under natural temperature fluctuations in Mexico City during the coldest winter experienced by the laboratory. He kept flies under outdoor winter temperatures from November 20 to January 22, when a night temperature of approximately 15.5° F. killed all the insects. During the 2 months before that date,

[9] See manuscript report 24, p. 153.
[10] See manuscript report 25, p. 153.
[11] See manuscript reports 53, 54, p. 153.

however, the flies had experienced a temperature of 32°, or below, on 20 occasions, and during 11 of the last 13 days of the experiment a mean minimum of approximately 23.8° was recorded in the cages. Yet during these 2 months only 6 males and 2 females of *Anastrepha ludens* died in the outside populations, whereas 2 males and 1 female died in the inside population held under optimum conditions. A total of 350 flies was involved, 50 of *A. ludens* and 100 each of *A. serpentina, A. striata*, and Mexican *A. mombinpraeoptans*. The other species proved less resistant to the low temperature than did *A. ludens*.

During the day the flies were active, but the maximum noon temperatures were not high. An average of 63.5° F. was reached at noon, but for several days in succession the peak was below 59°. These peaks were attained only for a short period at noon, the temperature for most of the day being lower. It seems evident, therefore, that the flies after experiencing fairly low temperatures at night can become normally active during the day if the temperature reaches 59° or above for a short time at noon. This is somewhat lower than the figure of 63.86° F. observed by Skwarra in the field, which is close to the average. It may be added that Stone has observed flies active and feeding in the laboratory during the morning with a temperature in the cages of 59° and 60°.

Although only a small number of adult flies were available, subsequent experiments were begun by Stone [12] on the same plan. Twenty *Anastrepha ludens* 1 month old, together with flies of other species, were placed outdoors. These were killed the same night by a temperature of 14.9° F. The following day 18 *A. ludens*, along with other species, were placed outdoors. That night a temperature of 17.15° killed 4 females. The following night 19.04° killed 4 of the surviving *A. ludens*, while the following night the remainder were killed by a freeze of 17.6°.

A further series of outdoor tests was carried on, and in these Stone found the minimum temperatures and the durations below 32° to be as in table 6.

TABLE 6.—*Minimum temperatures experienced by adults of Anastrepha ludens that ultimately survived and number of hours that the temperature ranged below 32° F.*

Experiment No.	Temperature	Time below 32° F.	Experiment No.	Temperature	Time below 32° F.
	° F.	Hours		° F.	Hours
7	21.56	4	11	23.18	5¾
8	22.10	6½	12	24.26	5¾
9	24.26	5½	13	27.95	4¼
10	21.92	8			

In all these cases the flies were exposed to temperatures much below freezing and to temperatures below 32° F. for considerable periods. In an earlier test (No. 6) a minimum of 15.8° F. was reached, which killed the flies and eliminated this test. Tests 7, 8, and 9 were conducted successively on the same population, so that this population experienced three successive shocks much below freezing. These are compared graphically in figure 41 with the temperatures experienced in the Rio Grande Valley of Texas during one of the worst cold snaps. It is evident, therefore, that adults of *Anastrepha ludens* can experi-

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[12] See manuscript reports 54, 55, p. 153.

ence heavy freezes and still survive.   From the results mentioned, it would appear that the temperature of a fatal freeze would approximate 17° F.

The flies in all these populations, with the exception of those in test No. 6, survived for many months afterward with no greater mortality than that shown in controls under optimum temperatures, and oviposited in fruit afterwards, producing many hundreds of larvae and adults.

To study further the resistance to cold, however, Stone [13] reproduced, by means of his variable temperature control apparatus (42, 43), a cold snap recorded at Weslaco, Tex., in March 1932, in which the temperature ranged from 30.2° to 44.6° F. for 108 hours.   The reproduction of the record was practically perfect during the first 3 days, although
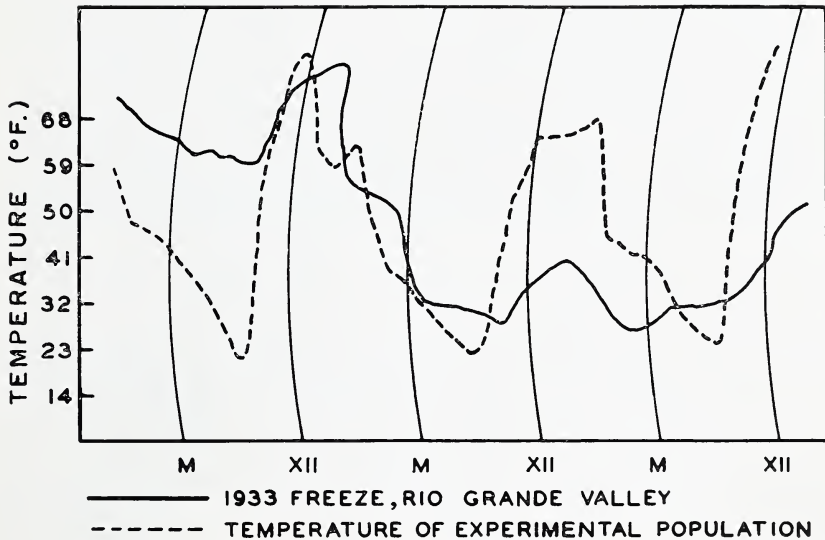
FIGURE 41.—Temperatures to which experimental populations of *Anastrepha ludens* were subjected in Mexico City compared with temperatures occurring in the Rio Grande Valley of Texas for 3 days in 1933.   M=Midnight, XII=Noon.

irregularity in electric current caused the temperature during the fourth day to fall somewhat below that recorded in the Valley.   The only important effect of this was to make the test more severe.   The test included 50 adults of *Anastrepha ludens* 103 to 113 days old and 50 adults 2 to 8 days old.   At the same time 50 adults of *A. serpentina* were included.   Air velocity in the cabinet was at 4.07 miles per hour. During the time of lowest temperature the relative humidity ranged between 41.7 and 49 percent.   The record of the temperature is shown in figure 42.

The first mortality readings were taken 7 hours after the close of the experiment.   They showed 18 adults of *Anastrepha ludens* killed or permanently injured among the older flies and 10 among the younger flies.   Ten days after the close of the experiment 48 percent of the old flies were dead, with 12 percent dead in the control, and 30 percent

[13] See manuscript report 71, p. 154.

of the younger flies were dead with no mortality in the control. The survivors, indistinguishable from control flies, continued to live and act in a normal manner. Although not all the *A. serpentina* adults were killed they proved less hardy than *A. ludens*.

In temperature studies one of the needs proved to be an instrument which would duplicate in the laboratory the standard weather records taken in any location. By such means it would be possible to duplicate the weather recorded in any locality in the United States
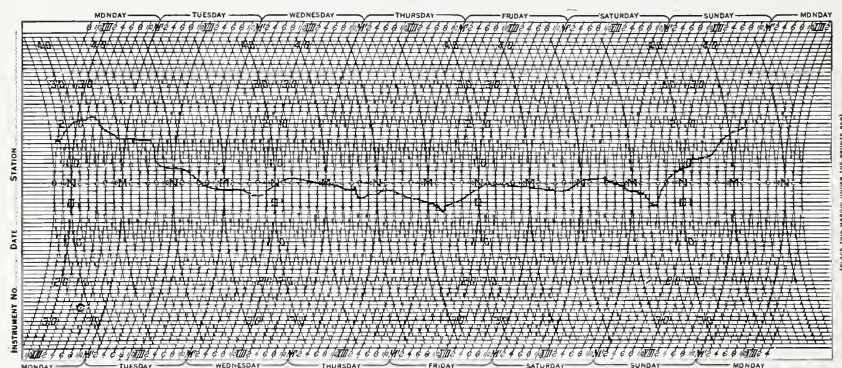
FIGURE 42.—Thermograph record of temperatures to which populations of *Anastrepha ludens* were subjected experimentally in Mexico City.

over a period of time and subject the flies to these conditions to determine their reaction. Obviously it would be impossible to transport the insects to uninfested areas to determine what the result would be.

Stone invented such an instrument, by which the usual thermograph record taken in any locality is utilized and the temperature with its fluctuations is followed in room, incubator, etc., over the period covered. A public service patent on the instrument has been obtained (*43*).
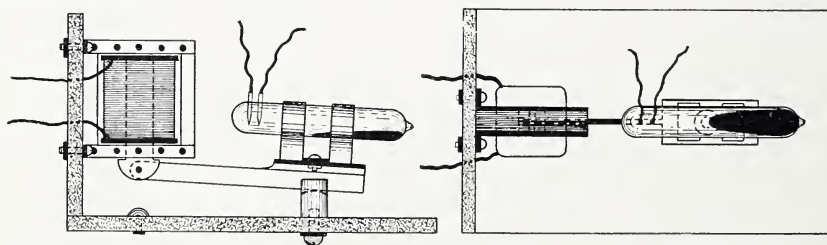
FIGURE 43.—Relay for temperature control for incubator, incorporating features designed by Ramírez.

With his instrument Stone has recently reproduced a winter season in Whittier, Calif. Not only did the original population of adult *Anastrepha ludens* survive and lay irregularly during the winter but a new population was built up from flies emerging.

In laboratory experiments on the effect of temperature on *Anastrepha ludens*, excellent control of temperature has been obtained by means of a rugged but sensitive relay incorporating features designed by Ramírez (fig. 43).

While *Anastrepha ludens* is usually thought of as a tropical species, it is evident from what has been said that it can withstand considerable low temperature, and it should be noted that it has not invaded the actual tropics.   (See p. 7.)

Moreover, the insects are often killed by high temperatures, especially if exposed to the sun.   When flies were being transferred for experimental work, high mortality has resulted from accidental exposure of the cages to direct sunlight for a period of time.   It has
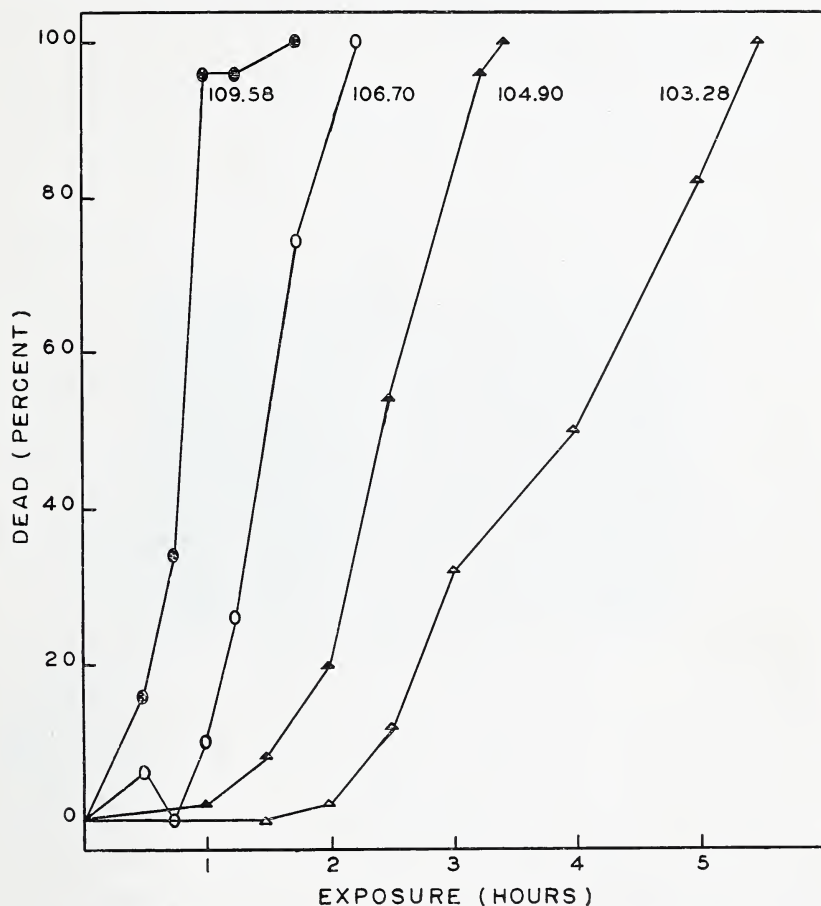
FIGURE 44.—Mortality of adults of *Anastrepha ludens* when exposed to different high temperatures.   (After Darby and Kapp (*13*).)

commonly been noted that flies under normal summer temperatures in Cuernavaca are less active at noon, but this may not be altogether due to temperature.

Skwarra [14] observed that flies always seek the shaded sides of leaves and fruit.   This has been repeatedly noted by others, Crawford (*9, p. 431*), however, observing them thus taking shelter only during the heat of the day.   In the Rio Grande Valley in Texas during the

[14] See manuscript report 24, p. 153.

infestation of 1936–37 large numbers of the fruits hanging inside the aprons of the trees were infested (fig. 7, *B*), whereas those exposed on the outside of the trees were much freer from attack. Baker[15] found the light reading inside these trees where infestation was so heavy to be 1 to 2 points, whereas on the outside of the trees it was 70 points, but no complete study of the light intensities selected by the fly has yet been made.

In 1900 Rangel, in Herrera et al. (*21, p. 77*), in line with experimental work in California, exposed adult flies to water vapor at 40° C. (104° F.), obtaining immobilization in 20 seconds and death at an exposure not indicated.

Darby[16] and Darby and Kapp (*13*) conducted experimental work in a very similar temperature range, using 103.28° to 109.58° F. but employing the usual incubator atmospheres instead of water vapor. A rapid kill was obtained at all temperatures used. The results are shown in figure 44.

Because of the records on the treatment of *Demodex* sp. in 1927 by infrared rays by Sheard and Hardenbergh (*37*), Baker tested adults first with a glowing coil in the usual reflector used for heating rooms, and later by a lamp so housed that visible rays were not directly emitted. But he had no equipment to segregate specific wave-length bands. In the first case he found rapid mortality; in the second it was only necessary to pass the flies, held in the fingers by a leg or wing, slowly across the path of the rays, an action requiring about a second, and they were dead. This effect he assumed to be due to the small bulk of the insects in conjunction with the penetrating nature of the rays. When only lightly dosed, flies gyrated as they do when affected by certain poisons. The rapid mortality obtained, while interesting, offered no practical application with *Anastrepha ludens*, since the method could not be applied to larvae in fruit and there seemed no possibility of applying it to adults in the field.

TRAPPING THE ADULTS

Any measure of adult activity is dependent on some method of record, and, with the opening of the Bureau's work, efforts were made to find methods of recording adult populations. Strips of sticky fly-paper hung in trees were used by Skwarra, and also by McPhail. The latter undertook work on traps, testing many different kinds of containers and devices, including modifications of commonly used glass fly traps. That which proved the most effective is shown in figure 45, and this has been adopted as the standard trap. The first samples made were blown in Mexico, and varied somewhat in size. The standard, however, is now made from a mold. The use of these traps with suitable lure now permits an index of adult populations and a method of inspection for adults.

The second problem involved, also attacked by McPhail, was that of the lures themselves. This was approached from two angles; (1) empirical tests of all materials known to be attractive to other flies, or of likely attractiveness, and (2) an attempt to isolate from materials showing attraction the active principle contained therein.

[15] See manuscript report 73, p. 154.
[16] See manuscript report 25, p. 153.

Results of studies of the first type were presented by McPhail[17] in 1933. These studies covered 495 different materials tested in the field in the following ways: (1) Using the standard type of glass trap alone, (2) using this trap with an extra container below, (3) using a screen-wire trap, (4) using an open quart can, and (5) using an open tumbler. The exposures ranged up to 15 days per test, and the recorded catch was used to indicate the possibilities of the materials.

Many of these materials attracted other insects. Sixty-nine of them showed some attraction to *Anastrepha ludens*, only two of them, however, to any marked extent. These two were essence of white wine and resinol spikenard. Space will not permit the tabulation of all the tests or even of all the materials.

At the same time that these extensive series were being run, Mc- Phail had under way studies with sugar solutions, fruit juices, and grain materials such as shorts, the last similar to the pollard lures used for other fruitflies. Earlier tests for *Anastrepha ludens*, in which sugar solutions similar to those employed in Texas were used,

FIGURE 45.—Glass trap adopted as the standard in work with *Anastrepha ludens* and other fruitflies.

were conducted by Plummer in Cuernavaca and indicated that such materials were worthy of extended study.

Following the work on miscellaneous materials, McPhail[18] devoted most of his energies to an effort to isolate an attractive ingredient from materials showing promise. The work was centered around several subjects, mainly the following: (1) Decomposing protein (*27*), (2) fermenting sugar solution, (3) yeasts in sugarless media, (4) cultures of various microorganisms from fruit and foliage, and (5) pollard lure.

The influence of ammonia in various reported lures and the fact that Mexican crude brown sugar in sodium hydroxide solution gave attraction to *Anastrepha striata* led to an extended study of protein materials with alkalies. The materials proved highly attractive to *A. striata* but gave little attraction to *A. ludens*.

Owing to the difference in ammonia evolved, gelatin was finally selected for comparison with casein; and, although the ammonia

[17] See manuscript report 42, p. 153.
[18] See manuscript report 60, p. 154.

measurements were greatly different, a heavy catch of *Anastrepha striata* was obtained with both. The casein lure was then studied separately, and the influence of the proportion of casein shown.

These protein studies did not result in the development of an attractive lure for *Anastrepha ludens*, but showed protein lures to be powerful attractants for *A. striata* and flies having similar responses, a fact confirmed by later work in Hawaii with the Mediterranean fruitfly.

The work on fermenting sugar solution centered around studies of (1) intermediate compounds of fermentation, (2) the effect of sulfur and methylene blue, (3) the effect of pyruvic acid and of acetaldehyde, (4) condensates, distillates, and extracts, and (5) adsorption tests.

Of the compounds known to occur in fermenting solution, only alcohol gave indications of attraction, and this very feebly. Tests with dilute pyruvic acid solution to which a small amount of yeast was added, as well as tests with acetaldehyde, acetylmethyl carbinol, and 2, 3 butylene glycol, indicated that the attraction observed was probably not due to pyruvic acid or to products in its reduction but to the yeast present.

However, the slight catch obtained with pyruvic acid solution led to tests in adding to fermenting solution compounds intermediate in alcoholic fermentation. The solutions were apparently toxic to the yeast, and the catches in not a few cases were high for *Anastrepha striata*, a fact suggesting the work on proteins.

This led to tests in which the pyruvic acid had been neutralized before yeast was added, which resulted in a catch as high as 953 against 369 for the standard fermenting control solution. Whether pyruvic acid is involved in the attractiveness of the standard fermenting lure remains to be determined.

The addition of small quantities of sulfur to the fermenting lure after it had been held for 5 or more days considerably increased the catch, although methylene blue reduced it. In the former case the odor of resulting hydrogen sulfide was distinctly noticeable, and the compound was presumably present in sufficient quantities to be toxic to the yeast. In all tests with fermenting solution the control was 80 gm. of granulated sugar, 1.5 gm. of dry brewer's yeast, and 1 liter of water. This is the formula to which other materials were added, as previously discussed.

Efforts of various kinds were made to obtain or to concentrate the attractive principle from this solution. Distillation did not give fractions as attractive as the original material. Condensates were equally disappointing. Attempts at extraction gave negative results. Adsorption experiments gave some indications. The addition of charcoal reduced attractiveness, and fermentation in the presence of charcoal resulted in a material which caught nothing. Attempts to recover an attractive material from the charcoal were unsuccessful.

While the standard solution contained yeast in sugar solution, giving the usual fermentation, preparations using yeast in sugarless media resulted in very good catches. This was the case, for example, when a small amount of sulfur was added, where the lure caught 464 flies against 350 for the control lure. Notable also was yeast in very dilute alcohol and yeast in water alone. The former was checked against the

control at various times in the year, and an interesting point, that there is a seasonal variation in the response of the fly to the material, became apparent. Summer tests showed the lure to be equal to the control in number of flies captured, while during the winter the material was hardly attractive. Results with other materials indicate that this might be true of a number of substances, including some of those discussed.

In view of the results just mentioned, work was undertaken with pure cultures of various organisms obtained in nature. Some of these were from the flies themselves. Others were from the fruit or foliage of mango or other trees in Cuernavaca. The organisms were plated and then grown in pure culture in different media for from 6 to 8 days before exposure in the field. Because of the fact that different numbers of traps and exposure days were used, the materials are rated per trap day.

The dominant organism always obtained abundantly from uninjured mango fruit in Cuernavaca was one giving a yellowish growth on the plates after some days. These bacteria also produced a slight odor of hydrogen sulfide. Cultures in broth when exposed in the field gave the highest rating of all tests, namely, a rating of 8 as against a rating of 4.7 for the control fermenting solution. Curiously, the same high rating was obtained for this organism in sugar solution even after the culture had been treated with copper sulfate just before exposure.

A yeast was found present on the mango fruit in small quantity by culture and, strangely, when this was grown in sugar solution the resulting rating was less than 1, whereas a stray yeast from plates in the laboratory, grown in the same way, gave a rating of 4.1, nearly equal to that of the brewer's yeast in the control solution. Bacteria cultured from plates contaminated by the flies themselves gave a rating of 3.1. The experiments with these different bacteria in comparison with yeasts are at least suggestive and warrant further consideration of the problem. The isolation and culture of the organisms were handled as an aid to McPhail by Baker, in cooperation with Mooser.

McPhail's early work with the lure made from wheat shorts indicated that it is almost as attractive as fermenting sugar solution, but not so dependable. It does not attract moths, a point of importance in some sections, as will be discussed later.

The question of the fermentation of this lure was checked by comparing samples sterilized chemically with unsterilized samples. Samples sterilized with mercuric chloride gave very low catches, as in other cases where this material was used. The use of alcohol, however, slightly increased the catch. Various other grain materials were satisfactorily substituted for the shorts, and in preliminary work McPhail got very favorable results with mill sweepings. The standard shorts formula used was 160 gm. of wheat shorts, 2 liters of water, and 30 gm. of borax.

Owing to the fact that shorts lures are usually light yellow, McPhail conducted a series of tests comparing light green, dark green, red, lavender, and light yellow. The light yellow colored lure caught more than double the number of flies taken in any of the other traps with the exception of the dark green.

In considering compounds of ammonia, McPhail carried out a series of 25 tests using a number of such compounds in water. Practically

all these captured some flies, although in none of them did the catch equal that from the fermenting control. The ammonia-vanilla lure found effective in Puerto Rico for *Anastrepha suspensa* (Loew) and *A. mombinpraeoptans* failed to give a good catch of *A. ludens* when tested on the hacienda in Santa Engracia.

In the early work extensive efforts to extract from the various parts of host plants materials that might prove attractive were unsuccessful.

In March 1934 McPhail studied adult activity in mango trees, using trap catches with fermenting sugar lure as the indicator, and measuring the following variables: (1) Percentage of total daily catch of each sex, (2) time of day, (3) mean temperature, and (4) evaporation rate. Later he made an analysis of his results (*26*), pre-
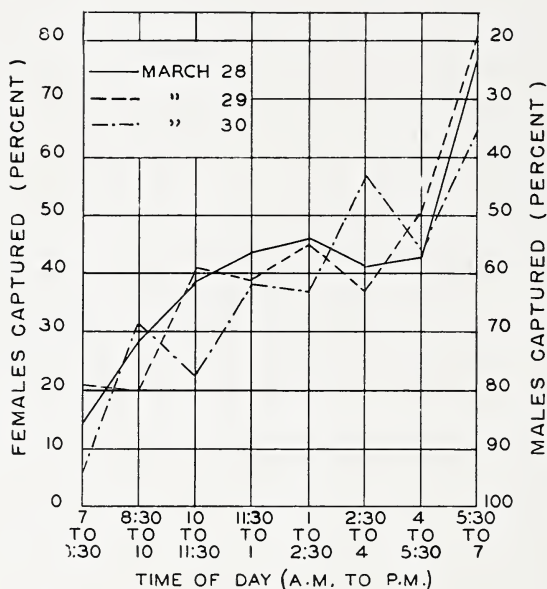
FIGURE 46.—Comparison of attractiveness of a lure to males and females of *Anastrepha ludens*. (After McPhail (*26*).)

senting regression equations for the linear relations for both males and females and curvilinear correlation as a test of the linear estimate. Figure 46 represents a comparison of the attractiveness of the lure to males and females, and figure 47 shows the relation of the various factors to the attractiveness of the lure.

The coefficients of total determination, 61.3 percent for males and 66.6 percent for females, show that a considerable part of the total variance had not been accounted for, but the coefficients of partial correlation give temperature as the most influential of the measured factors on both sexes, time of day having an important influence on the males but being only third in its effects on the females, while evaporation was second in importance with the females but of least effect on the males. McPhail concluded that the observed differences between the sexes may be due to the influence of the oviposition re-

sponse in the females, and incidentally called attention to the fact that differences in the proportion of sexes caught by a lure may not be due to the lure itself.

As previously mentioned, the catch of moths in fermenting solution is often something of a nuisance, and probably reduces the trapping efficiency of the material, since the presence of many moths causes the lure to dry up in the traps. As a result, therefore, experiments
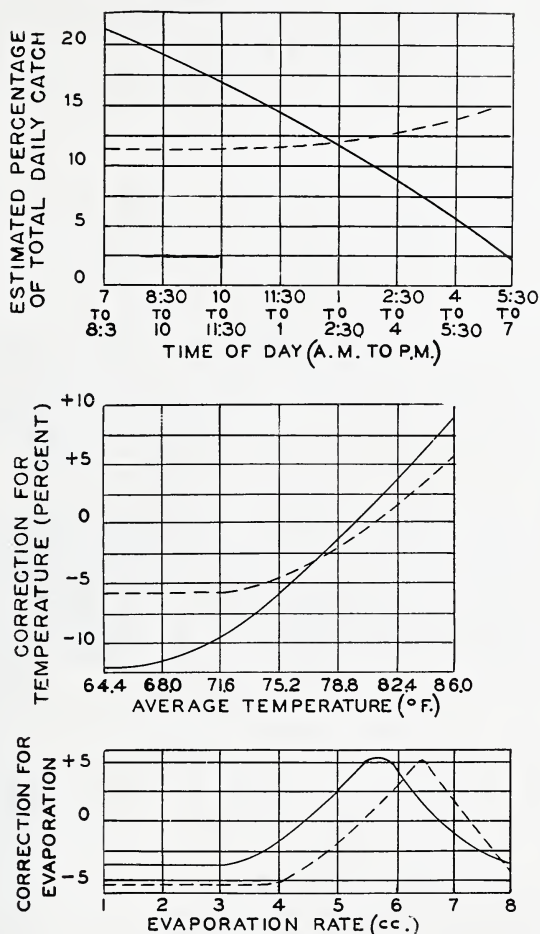
FIGURE 47.—Relative importance of different factors in the attractiveness of a lure to *Anastrepha ludens*. The solid lines represent males and the broken lines females. (After McPhail (*26*).)

were undertaken by McPhail to determine the influence of screens of different mesh and location in preventing moths from entering the mouth of the trap. Tests were made at Hacienda Santa Engracia under the following conditions: (1) The standard glass trap without screen; (2) screen of 4-mesh-to-the-inch hardware cloth, placed on the outside of the mouth of the trap; (3) the same screen placed on the inside of the trap; and (4) a screen 3 by 3⅓ mesh to the inch

placed inside the trap. The results at three different time periods are shown in table 7.

TABLE 7.—*Comparative catch of adults of Anastrepha ludens in glass traps with and without screening*

Trap rig	Fly catch		
	First exposure	Second exposure	Third exposure
	Number	*Number*	*Number*
Without screen_____	64	57	75
4-mesh screen outside trap_____	4	10	30
4-mesh screen inside trap_____	4	10	54
3- by 3½-mesh screen inside trap__ _____	9	26	66

It will be noted that the unscreened trap far outstripped the others, and that traps with screens outside caught fewer than those with screens inside. These results are in keeping with earlier experiments by McPhail in Cuernavaca, all of which indicated that anything at all obscuring the mouth of the trap tends to reduce the catch. Where at all possible, therefore, open traps without screening mechanism of any kind should be used. The flies enter the traps slowly, gradually moving upward, and when anything appears in their path they turn and work away from it. At Santa Engracia the senior author has observed flies to turn on numerous occasions when reaching the screen and subsequently to make no further effort to enter.

Another condition, often of considerable importance, is the heavy growth of scum in the traps. In the field this has been observed to reach a stage in which the sugar lure becomes almost like thin jelly. On the hacienda this condition was found in nearly all screened traps, and it is assumed that the absence of larger insects from the traps may have something to do with the ability of one organism so to dominate the lure.

MIGRATORY MOVEMENTS

The migratory movements of the flies have not been fully determined. It was at first supposed that they move about very little, since the movements observed were very short flights. Skwarra then found them in different locations—for example, in a corn planting, as previously mentioned. The spread of *Anastrepha ludens* by adult flight is naturally limited, among other things, by extremes of temperature. Flies are very seldom taken in light traps, as are many other insects, although they are positively heliotropic. At least this response is definitely shown by laboratory populations during the day. It may be that night temperatures are a factor in their movements.

The movement of flies from mango trees, after the fruit had fallen, to guava bushes in fruit has been discussed (p. 30) as has the movement of populations to and from citrus groves in Santa Engracia (p. 32).

It is exceedingly difficult to determine how far individual flies may emigrate. The customary practice in such determination, i. e.,

the marking and release of large populations and their later recovery, is not available, since regulations aimed at depressing fly populations are in force in the various infested regions in Mexico.

Probably the most definite data have been obtained under Hoidale's direction in the trapping work south of the Rio Grande. This work resulted in captures in such wild land as that shown in figure 8, *D*. At the same time, it is known from the Rio Grande Valley records that the flies leave there in the spring. The season of 1936–37 was very instructive since a heavy infestation took place and flies of the spring generation were observed emerging from the soil. The migration from the groves was already under way, and apparently these newly emerging flies joined this movement.

The catches in the wild land south of the border can be interpreted accurately only with detailed knowledge of the distribution of *Sargentia*. This is the only wild native host so far known in that region. A survey to determine its exact distribution is under way. Apparently, however, flies are captured in brush land lacking this fruit, which indicates a general movement of flies emerging from this native host.

Carriage by air currents has been suggested, this factor having been discussed by Baker as early as 1927, but here again interpretation would depend on exact knowledge of sources of native hosts, and the capture of adults in the air would indicate only their occurrence in the region of capture, as does their capture in traps.

Length of Adult Life

The first studies at the Mexican laboratory on the length of life of adults were made in the insectary in Cuernavaca by McPhail and Bliss (*29, p. 20*), who found some flies still living at 179 days when the series was discontinued.

The work was then taken up by Kapp [19] on populations maintained in the laboratory in Mexico City. She found that flies may survive for many months and that under the conditions of her experiments males lived much longer than females. The longest life recorded by her was 11 months for 3 females and 14 months for a male. The best comparison in her work is shown in figure 48. These flies, however, were 2 months old when the series was started, as indicated by the light lines in the figure. The graph represents a population of 250 females and 220 males.

Darby and Kapp (*14, p. 6*) suggest that withholding of eggs may affect the health of the flies and so shorten the life of the females. Just the contrary, however, appears to be shown by Stone's data on *Anastrepha serpentina*. The flies that lay the most appear to die the soonest.

Stone continued Kapp's records,[20] finding, as she did, that the males live the longest. At 16 months only four flies were left alive, all males.

Control of the Adults by Sprays

The first toxicity tests at the laboratory in Mexico were made with copper salts, following the work on copper with the Mediterranean

[19] See manuscript report 21, p. 153.
[20] See manuscript report 35, p. 153.

fruitfly in Florida. Kapp [21] carried out cage tests in Mexico City, and Stone [22] conducted spray tests in Cuernavaca.

Kapp reported results with 1, 2, and 5 parts per 1,000 of copper carbonate and 1 part per 1,000 of copper chloride. Little kill was obtained with the carbonate, flies being alive after 36 days, whereas in 5 or 6 days all those feeding on the chloride were dead. Twenty-five grams of granulated sugar and 50 cc. of maple sirup were used per liter. No other food was available. The poison was fed on small pieces of absorbent cotton.
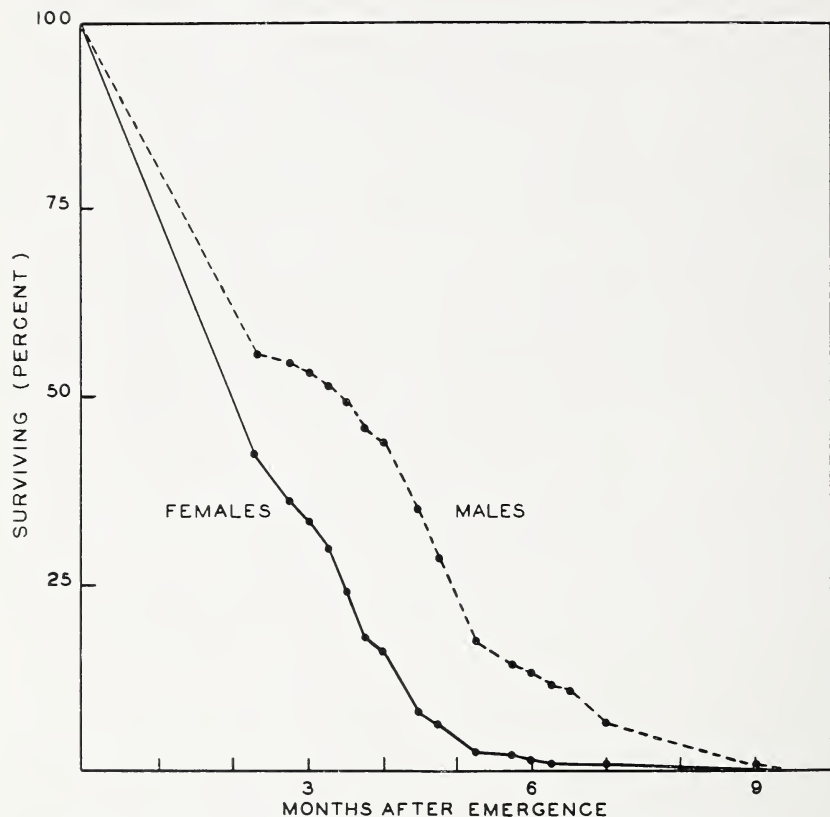
FIGURE 48.—Length of adult life of *Anastrepha ludens* in the laboratory at Mexico City. (After Darby and Kapp (*14*).)

Stone and Plummer used copper sulfate in the standard sugar-sirup mixture, spraying mango trees at 10-day intervals. No mortality resulted, as was reflected in subsequent fruit infestation, since the several thousand drops examined all contained larvae. Cage tests checked by Stone against the spraying showed no mortality during 7 days. He concluded from preliminary observations that the adults will not feed on the sprayed foliage when fruit is available, because only in cages containing sprayed foliage without fruit did he obtain a satisfactory kill.

[21] See manuscript report 23, p. 153.
[22] See manuscript report 28, p. 153.

Plummer [23] continued this work, using a number of copper compounds at the rate of 8 pounds in 200 gallons of solution containing 25 pounds of sugar and 5 gallons of molasses. The experiments were run in cages. Flies exposed to copper sulfate in the presence of cut orange lived 3 or more weeks. The copper carbonate was less effective, since some flies survived 13 days in the presence of the spray alone. Cupric chloride killed in 6 days in agreement with the preliminary tests by Kapp. Cupric arsenite killed in 1 to 4 days in the absence of food, in 3 days in the presence of mango, and in 6 days in the presence of cut orange. Cupric aceto-arsenite killed all flies in 3 days in the absence of food and in 8 days when fruit juices also were available.

In view, however, of the success obtained in Florida with copper carbonate against the Mediterranean fruitfly, experiments with this material were carried through by Plummer,[24] 1,800 insects being used. Experiments were designed to determine mortality in the presence and absence of food, and cut orange was introduced 12, 24, 48, 72, and 96 hours after the beginning of experiments. The series with and without cut orange appeared to give no consistency, the mortality being sometimes as high in the presence of the fruit as in its absence. Survival continued for a month or more, showing rather clearly that any hope of using this compound as a standard spray would have to be abandoned.

Mortality obtained in an extended series is shown in figure 49. The data are plotted in probits (Bliss (*3*)) for comparison with the regression lines shown for other materials of which the toxic effects are pronounced. Where toxic effect is distinct a rectilinear relation is evident.

Since the effect of the copper carbonate on *Ceratitis capitata* in Florida was assumed to be due to its action on the intestinal flora of the adult, studies were begun by Mooser and the senior author on the intestinal flora of *Anastrepha ludens*. Smears of the intestinal content revealed abundant bacteria, and serial sections of entire flies were prepared for study of the locations of these bacteria preparatory to toxicity work. The sections showed the bacteria in abundance.

As a result of the inefficiency of copper carbonate just discussed, preliminary work was begun by Plummer [25] with nicotine sulfate containing 40 percent of nicotine as a poison, and this was continued with large populations, and with the molasses content varied from 1 to 30 percent. Sugar was not used. Results with high percentages of cane molasses were unsatisfactory, evidently owing to the dilution of the poison in the meal. With 1:300 nicotine sulfate and 5 percent molasses, however, 100 percent mortality was obtained with foliage that had been sprayed 33 days previously. These experiments were conducted in Cuernavaca when the humidity was low, and they appeared so promising that Plummer [26] made an extended study of this material. When foliage had been held for 43 days after spraying and then offered to adults of *Anastrepha striata*, 100 percent mortality was obtained in 5 to 6 days, and even after the sprayed foliage had remained 70 days 65 to 70 percent mortality of adults of *A. ludens* was

[23] See manuscript report 30, p. 153.
[24] See manuscript report 38, p. 153.
[25] See manuscript report 33, p. 153.
[26] See manuscript report 36, p. 153.

obtained with it in 7 days, and 87.5 to 97.5 percent in 19 days.   This was with a dilution of 1 : 200, and with as high as 20 percent of molasses. With a dilution of 1 : 300 and 10 percent molasses, 100 percent mortality of adults of *A. ludens* was obtained in 5 days after the sprayed foliage had been held for 13 days.

In view of findings of this order, it was believed that the molasses-nicotine sulfate mixture was unusually effective, especially since it
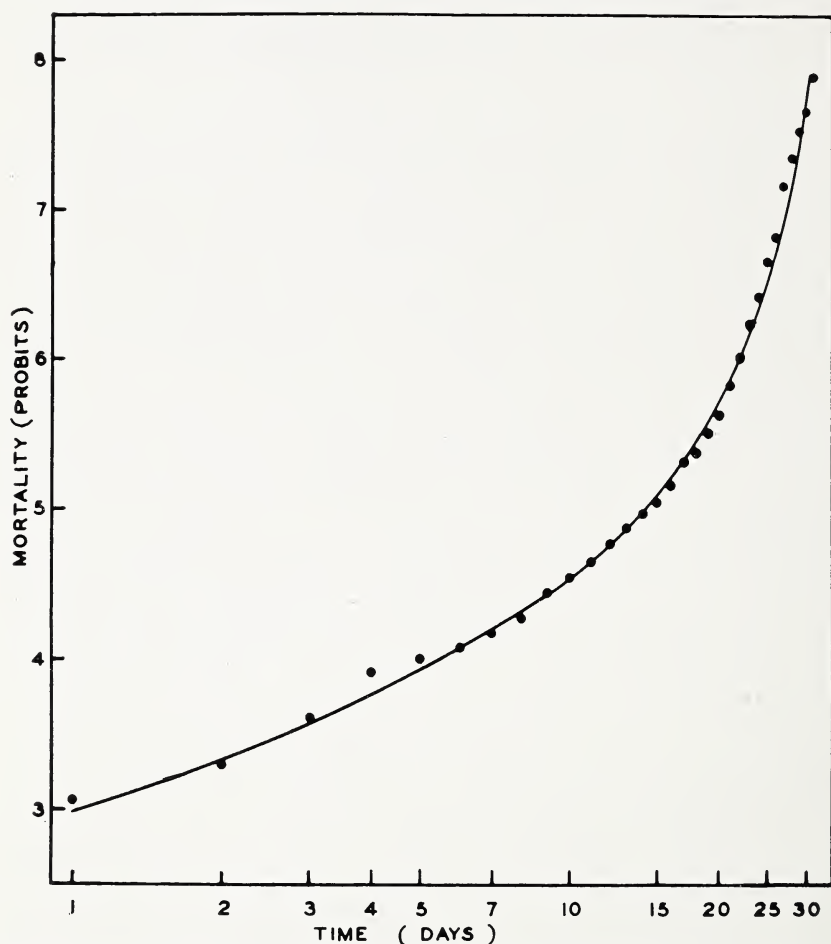
FIGURE 49.—Mortality of adults of *Anastrepha ludens* produced by 8 pounds of copper carbonate in 200 gallons of solution containing 25 pounds of sugar and 5 gallons of molasses.

had been held on the foliage under atmospheric conditions of low humidity.

While every confidence was felt in these extensive experiments carried on in Cuernavaca, Plummer continued the work in Mexico City, where tests could be carried out under controlled conditions of temperature and humidity, and where much higher temperatures could be used.

The technique in Mexico City employed smaller cages 7¼ by 12 by 12 inches and pebbled glass plates 4½ by 5$\frac{9}{10}$ inches instead of foliage, so that the sprayed area would remain constant. Longevities under the two sets of feeding conditions were first compared and found to be in fairly satisfactory agreement. In most cases the kill was slightly more rapid with the plates and small cages.
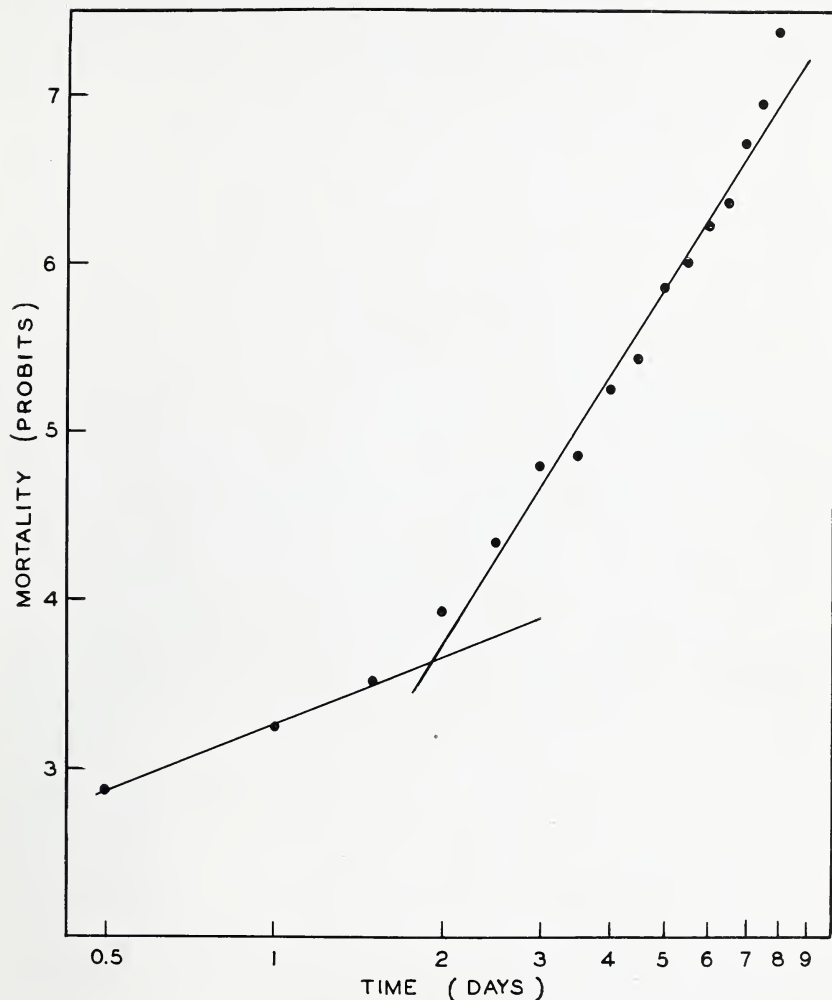
FIGURE 50.—Mortality of adults of *Anastrepha ludens* produced by nicotine sulfate spray.

As an example of the nicotine kill, a group of three runs was chosen at random and totaled, the results being plotted in figure 50. These runs were begun on September 13 with flies that emerged September 9. They contained plates sprayed with 5-cc. portions of 1:200 40-percent nicotine sulfate with 5 percent of blackstrap. The plates had been run in previous tests; therefore the quantity of material had

been reduced by previous feeding. They had been sprayed 10 days previous to the experiments, which were carried out under controlled conditions at approximately 77° F. and 50 percent relative humidity.

As the question of change in the nicotine-molasses mixture after the water had become evaporated subsequent to spraying was more important than any changes with time in the spray solution itself, a series of freshly prepared solutions having a range from pH 2.89 to 7.53 was made up and sprayed upon plates. After being held 160 days these plates were washed and determinations made. The result was a graded series with the lowest at pH 5. Parallel toxicity tests showed that the toxicity of the material remained fairly uniform up to about pH 6.3, but that it began to drop off rapidly above pH 7.

The influence on efficiency of higher temperatures to which sprays might be subjected in the field was checked under artificial temperatures, and results found to be satisfactory.

The question of high humidities was then attacked, largely to round out the results. The findings were surprising, since at high humidities both toxicity and nicotine content of the sprayed material fell off rapidly. Sprayed plates were held for various periods up to 88 days and at relative humidities up to 80 percent. Tests with a home-made turbidimeter and a silicotungstic acid method devised by Baker showed increasing loss of nicotine as the relative humidity increased. For example, after 21 days' holding at 20 percent relative humidity the nicotine test still remained good, whereas a comparable plate after 23 days at high humidity showed no nicotine remaining. The tests for nicotine were in rough agreement with the toxicity findings at the dilutions that would be represented, and, since very high humidities are often met with in the field, especially in locations like the Rio Grande Valley, it became evident that the nicotine spray using nicotine sulfate would not give the holding power all the earlier studies with it had indicated. Information available when the original nicotine sulfate work was in progress had indicated that conditions of low humidity and high temperature would be the most severe on the spray, and conclusive results under those conditions had been obtained. The laboratory findings on nicotine had built up tests on approximately 10,000 flies.

Owing to the findings with high humidity, Plummer began experiments with compounds of nicotine other than the sulfate, since the kill with nicotine was obviously high. Few of these experiments up to the present time have been extensive.

Tests with nicotine tannate, prepared by the method of Headlee, Ginsburg, and Filmer (20), indicated that the material stands up better than the sulfate under the conditions required. Nicotine binoxalate gave a rather low mortality and appeared therefore not to be promising. Nicotine humate, as prepared by the Insecticide Division of the Bureau of Entomology and Plant Quarantine, appeared promising if applied in double the proportions usually used, the thicker coating apparently having an influence on the release of the nicotine. Nicotine bitartrate, as prepared by the same Division and containing 32.6 percent of nicotine, appeared promising, since a good mortality was obtained after sprayed plates had been held from 24 to 62 days, longevity on the sample after 24 days being 2.2 days.

On the hacienda where spray plots were laid out, the conditions for

the holding of the nicotine-molasses mixture were adverse. The valley is often misty and on many mornings the trees are wet. It was rather expected, therefore, from the results of the experiments previously discussed, that the material would have little effectiveness under such field conditions.

Data were obtained between December 13 and April 14 from a plot of approximately 100 young Valencia orange trees which were sprayed 9 times with concentrations of nicotine sulfate (40 percent) ranging from 1:60 to 1:200 and with 5 to 10 percent blackstrap molasses. The control was of similar size. Populations were measured by means of 24 glass fly traps in each plot. Throughout the season there were consistently fewer flies in the sprayed plot than in the control, although the actual reduction never reached much above 50 percent. The reduction in population was somewhat greater in a smaller plot sprayed twice with lead arsenate at the rate of 4 pounds in 100 gallons of solution containing 4 percent of blackstrap molasses.

These plots of young oranges were not satisfactory for an adequate study of the toxic effects of the spray, owing to the small populations and the general movement throughout the groves. The results appeared of value, however, in giving some idea of what might be expected in sprayed groves sparsely populated by moving flies. While only part of the effect can be definitely assigned to the spray, the trend in population was obviously downward. Under these adverse conditions nicotine sulfate gave an apparent seasonal reduction of 38 percent as against 49 percent for lead arsenate. The results with nicotine bitartrate on a similar plot were less satisfactory, amounting to only 24 percent.

These figures indicated that under the conditions existing the nicotine sulfate-molasses spray could not be expected to reduce populations sufficiently to prevent infestation of the fruit, and were in keeping with the laboratory results at high humidities. Nevertheless it was thought advisable to carry a sulfate plot another season. Nicotine sulfate (40 percent) was used at the rate of 1:200 with 10 percent blackstrap molasses. Accordingly population studies were made in proposed plots and controls during early fall, and for the sulfate plot as nearly comparable conditions as possible were selected with 244 orange trees in the spray area and 254 in the control.

This plot, however, was not satisfactory after the season progressed, since very small numbers of flies later migrated into it and reduction in the sprayed plot appeared to mean little. At various times a small fluctuation in the population would make the difference between practically no control and a very high one. It seemed obvious, however, that other materials under study were so much more promising than nicotine sulfate that the efforts should be concentrated on them.

Baker had carried out preliminary tests with various materials. The units in these and other tests were 40 flies. Sodium copper carbonate prepared in the laboratory gave a complete kill in 8 days, but in sunlight it rapidly broke down. Copper tartrate gave a kill in 5 days. Potassium copper tartrate was made in the laboratory, but it changed rapidly and required 16 days to kill. Copper tannate, or what was presumed to be this compound, caused very little mortality, al-

though tannic acid in sirup gave a kill in 7½ days. A mixture of copper carbonate at the usual rate of 8 pounds per 200 gallons and about the same amount of cream of tartar and 10 percent sirup gave results remarkably different from those given by the copper carbonate alone, complete mortality being obtained on the third day. The mixture of copper carbonate and cream of tartar was then held for 10 days and again tried. The toxicity had become very greatly reduced. Copper citrate, 4 pounds in 100 gallons of solution, required 16 days to kill. Compounds of zinc gave little mortality beyond the controls, and uranium potassium tartrate required 31 days to kill. The two most promising poisons were thallium and antimony, the latter in the form of tartar emetic. The former, however, was ruled out because of recorded injurious action on vegetation. Owing to the similar physiological effects on animals of arsenic and antimony, it was feared that antimony compounds would affect fruit ratios as does arsenic. The determination of this point was undertaken on a cooperative basis by the Bureau of Plant Industry.

The preliminary results from tartar emetic, at the rate of 4 pounds in 100 gallons of 10 percent sirup solution, were very good as far as toxicity was concerned. Tartar emetic gave complete mortality in 2 to 3 days with both *Anastrepha ludens* and *A. striata*. The regularity of toxic action, as well as the kill obtained, was promising if the physiological effect on fruit should prove not to be detrimental. In the laboratory in the Canal Zone, Zetek had previously found high mortality with the species there, and as a result of his work tartar emetic sprays for fruitflies appeared to offer unusual promise. Insoluble antimony salts tested, however, gave little mortality.

The fact that dusting for the rust mite is a common practice in many regions led Baker to include some preliminary tests with sulfur. When 200-mesh 80-percent sulfur was used, little effect was shown in the first trials, but others showed some mortality the day following the dustings. The flies were held in cages in the regular way, and the sulfur was dusted into the cages, which were then placed in a warm location to simulate the effect of hot days. Some of the flies were heavily coated, but others apparently escaped contact with the powder. It seemed evident that heavy dusting would produce some mortality of the flies present, but not a sufficient kill to be of service in control.

Extracts of chrysanthemum flowers in 10 percent sirup gave mortality during the first 4 days, but little later. Tests with a definite content of pyrethrins did not give complete mortality until the population had fed for 11 days.

Baker then tried rotenone in a dilution of 1:1,000 with the usual 10-percent sirup, and this gave a complete kill by the fifth day. Complete mortality on the fifth day was also obtained after the sprayed plate had been held 6 days in diffused light and used a second time. Since exposure to sunlight, however, reduces the toxicity of rotenone, studies with it were not developed.

The action of rotenone in paralyzing the flies, but not immediately killing them, was marked even after a plate had been held a week and run a second time. This action appeared to be due to ingestion of small quantities. A similar action was obtained from an alcoholic extract of cebadilla used in the usual sirup solution. This gave a complete kill in 4 days. When run again after a week's time the

sprayed sample required 5 days for complete mortality, but paralysis was much greater on each day than on any day previous.

During a visit to Oaxaca, samples of a plant called mata de perro were obtained. Alcoholic extracts of this plant killed slowly, but also had a paralyzing effect. Plummer, in his work with hierba de cucaracha (*33*), found a similar paralyzing action to be very marked, as will be mentioned in the discussion of that plant.

Baker also carried on work of a different character, using the toxins of pathogenic bacteria. The ones employed were the toxins of tetanus, diphtheria, and gas gangrene. No positive results were obtained with the flies.

Attention was then turned to vegetable products resembling toxins. A preparation of ricin was made from castor-bean seed, hulled and pressed, and was used in a 10-percent sirup mixture. No mortality was obtained beyond that of the controls.

The toxicity of such materials is rather easily modified, and this point was checked. The ricin preparation was tested on goldfish and gave no kill of the fish. It acts as a vegetable agglutinin, and the preparation was, therefore, tested on mammal red cells. It agglutinated in dilutions up to one two-hundredth of the original solution. But when this was tried on goldfish red cells no agglutination took place, even with the original solution.

The venoms from poisonous snakes closely resemble materials such as ricin and bacterial toxins, but no venoms were available at the time Baker was carrying on his studies. Later Plummer obtained a sample of rattlesnake venom through the kindness of Mooser, but with it he obtained little mortality of *Anastrepha ludens*.

The studies just mentioned appeared to indicate that such materials are rather inactive on the flies when used as food poisons, which is the only method that would be of any practical value. Baker therefore turned his attention to aqueous extracts of plants which produced foam and hemolysis in vitro. Saponins were assumed to be the agents involved, and it was desired to learn if these hemolytic agents were inactive on the flies, as were the poisons of the type previously mentioned. Extracts were prepared, using 25 gm. in 300 cc. of water, and of these a 20-percent dilution was used with 10 percent of sirup. *Saponaria* root so treated gave mortality in preliminary tests about equal to that of lead arsenate, at the rate of 8 pounds to 200 gallons with 4 percent blackstrap molasses. Panama bark handled in the same way and used in 10-percent dilution gave a slightly slower action. That a consistent toxic effect was produced by these materials is shown from figure 51, which is plotted from the total figures obtained from the three runs made with Panama bark extract in 10-percent dilution.

On the assumption that this action was directly due to the saponin, a part of the 10-percent solution was shaken with a solution of cholesterin in acetone and the acetone allowed to evaporate. The extract so treated gave practically no mortality, the results being of the same order as those obtained from water, cholesterin, and acetone prepared in the same fashion.

Commercial saponin of pure grade, therefore, was used in 1-percent solution with 10 percent of sirup and gave a mortality slightly slower than that from lead arsenate. Dilutions of 0.5 percent with 5-percent sirup and 0.02 percent wth 10-percent sirup were then tried,

The former gave complete mortality in 7 days, the latter in 10 days, whereas the 1-percent solution had produced a kill in little over 3 days.

Unlike these results, however, were those obtained from an extract of shi-shi, a product of the agave plant used in Mexico for washing clothes on account of the abundant foam produced. The extract gave indications of a very high saponin content, and in 1-percent dilution killed goldfish more rapidly than the 1-percent strength of *Saponaria* extract, but a 10-percent dilution gave no mortality of flies beyond that of the control. The extract gave a reading of pH 5.8, and
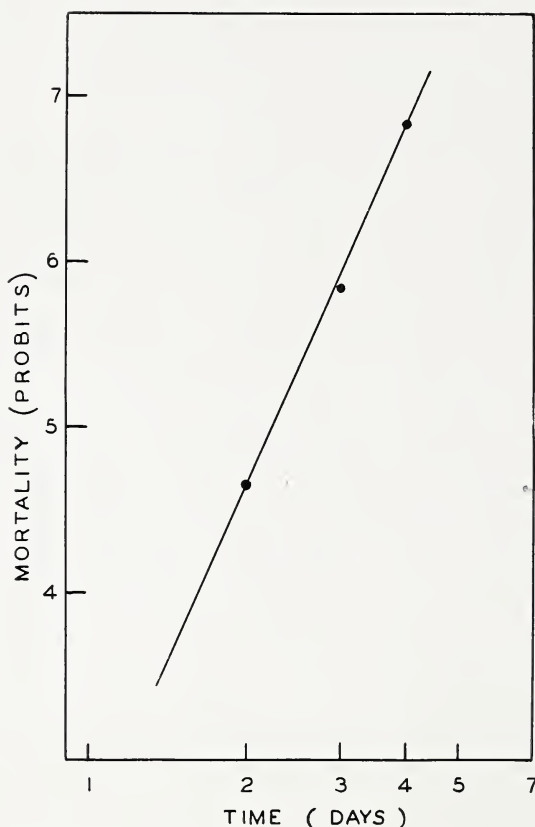
FIGURE 51.—Mortality of adults of *Anastrepha ludens* from the use of 6.95 pounds of Panama bark in 100 gallons of solution containing 10 percent molasses.

on testing the other substances a lowered pH value resulted in a kill of goldfish that was increased, whereas the toxicity to the flies was decreased.

The tests mentioned were made with *Anastrepha striata*, since no *A. ludens* were available at the time. Later they were repeated with adults of *A. ludens* from two different sources, and a very much slower mortality rate resulted. A 1-percent solution of the same *Saponaria* sample required 9 days to produce complete mortality, instead of the 3 days with *A. striata*. In these latter tests a different sirup was used,

owing to the exhaustion of the former supply, and the effect of the sugar in inhibiting saponin action was therefore tested, using Protozoa. The sugar did not appear to be involved in the results.

In this phase of the work the senior author had the assistance of Mooser, through whose kindness the bacterial toxins were obtained, and that of Julia Baker, who did work with the various materials on Protozoa and who carried the studies somewhat farther, although the results are not here reported since they had no immediate bearing on the development of a poison spray for *Anastrepha ludens*.

Plummer, subsequent to his earlier work with copper sulfate, copper carbonate, and nicotine sulfate, conducted preliminary work with many materials at 77° F. These were compared with lead arsenate, 8, 4, and 2 pounds per 100 gallons, which gave an average length of life of 3.42 days in the first concentration containing 4 percent of black-strap molasses, 2.85 (*Anastrepha striata*, 10 percent molasses) and 1.70 (2 percent molasses) in 2 series in the second, and 3.55 days (*A. striata*, 10 percent molasses) in the third. At 8 pounds with 2 percent black-strap molasses, cupric nitroprusside gave 4.39 days; at 4 pounds with 10 percent molasses, 4.42 and 2.65 days. Copper hydroxide and zinc hydroxide, 4 pounds to 100 gallons with sugar added, gave 4.17 days.

Tests were continued at 77° F., and compounds were used at the rate of 4 pounds in 100 gallons of solution containing 10 percent of molasses. Cupric salicylate allowed a length of life of 1.69 and 2.35 days; cupric bromide, 1.92; cupric perchlorate, 1.77; cupric ammonium chloride, 2.12 and 2.65 days; cupric chloride, 2.37 and 2.72; cupric phenate, 2.02; cupric hydroxide-aniline chloride, 3.72; cupric potassium phthalate, 5.4; cupric tartrate, 5.57; cupric formate with 5 percent molasses, 2.81 days; cupric lactate with 5 percent molasses, 2.35 days; soluble cupric tartrate with 1 percent molasses, 3.14 days; with 2 percent molasses, 2.21 days; and with 5 percent molasses, 2.63 days. Bordeaux mixture, 3–3–50, with 1 percent molasses, gave 2.72 days. The probability of injury to citrus through application of some of these highly soluble materials and reduction to the nontoxic cuprous state by reducing sugars in molasses led to the discarding of these materials.

Other compounds of copper which gave rather slow kills were cupric potassium chloride, cupric molybdate, cupric oxalate, cupric oleate, cupric chromate, cupric phosphate, cupric benzoate, and cupric stearate.

During his work on different copper compounds Plummer [27] conceived the idea of combining sugar and copper in the same manner that sucrates of strontium, barium, etc., are made. The result was the development of copper sucrate, a new material as an insecticide, and the granting of a public-service patent covering the product (*32*).

It was thought that with the sugar and copper apparently combined chemically no sirup or other sweetening would be required when the material was used as a spray. At the same time different proportions of sucrose could be used in making it. Tests were conducted with adults of *Anastrepha mombinpraeoptans*, *A. ludens*, and *A. striata*, using different percentages of sucrose, and copper sucrate was forwarded from the Mexican laboratory to those in Honolulu and Puerto Rico for similar tests. Plummer's laboratory tests covered 22,000 flies exclusive of controls.

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[27] See manuscript reports 41 and 62, pp. 153, 154.

While results were somewhat variable, they were promising, since a copper sucrate with 73 to 75 percent of the standard quantity of sucrose killed in an average of 3.5 days as compared with 2.89 days for tartar emetic. In the tests there was survival up to 10 days, but the numbers used were large so that survival over longer periods might be expected.

Copper sucrate gave a very good kill also at the other laboratories where it was under test, and this promise indicated the advisability of field tests in comparison with other insecticides. Spray plots were therefore set up in Santa Engracia and sufficient material obtained for field spraying. Detailed results on this phase of the work are not yet available.

The data on copper sucrate taken by McBride and Marlowe in Hawaii with the Mediterranean fruitfly show that it is more toxic to *Ceratitis capitata* than it is to *Anastrepha ludens* or other species of *Anastrepha* tested. To *C. capitata* it is sometimes more toxic than lead arsenate. This point is of interest, since copper carbonate proved toxic to the Mediterranean fruitfly but was of practically no value against the Mexican fruitfly. In Florida the theory was developed that the toxicity of copper to the Mediterranean fruitfly was due to its action on the intestinal flora, although that theory was not followed through to proof. The fact that the copper sucrate kills *C. capitata* much more rapidly than it does *A. ludens* adds another bit of evidence to the general action of copper on *C. capitata* and added proof of the resistance of *A. ludens* to slightly soluble copper insecticides in general.

Miscellaneous tests were continued at 77° F. Tribromophenol at approximately 8 pounds with approximately 5 percent of blackstrap molasses per 100 gallons gave an average life of 3.61 days. Using these same concentrations, *b*-naphthalene-sulfonic acid gave 2.80; p-nitro-chlorobenzene, 1.95; and dinitrophenol, 2.03 days. "Anabasine sulfate" at 1 gallon per 100 with 5 percent of blackstrap molasses gave 4.13 days; at ½ gallon per 100 with 5 percent of blackstrap molasses, 3.56 days. Picric acid at 4 pounds with 10 percent of molasses gave 3.83 days when tested with *Anastrepha striata*; 4 pounds of urotropine and 1 percent of molasses, 3.86 days; and a material apparently containing cube extract, 0.5 gallon with 10 percent of molasses and 2 percent of 0.1 molar sodium hydroxide, 1.55 days.

Cryolite, believed to be the synthetic product, and mixed at the rate of 4 pounds with 20 pounds of granulated sugar in 100 gallons of solution, gave a fairly good kill at 77° F. The toxicity curve is shown in figure 52, *A*, for a summation of 6 runs. Natural cryolite was later used by Plummer extensively in field trials at Hacienda Santa Engracia. Very large plots were sprayed and trapping records obtained. The results were far from satisfactory, since very little population reduction was shown. The question of the natural product vs. the synthetic product, however, requires further consideration.

Slow mortality was recorded at 77° F. for the following compounds, each in 100 gallons of solution: 4 pounds of barium fluosilicate with 20 pounds of granulated sugar; 4 pounds of barium chloride with 10 percent of molasses; 4 pounds of barium manganate with 10 percent of molasses, using *Anastrepha striata*; 4 pounds of barium sulfate with 10 percent of molasses, using *A. striata*; 8 pounds of barium sucrate

with 2 percent of molasses. Barium hydroxide, however, at the rate of 8 pounds with 2 percent of molasses gave an average life of 2.76 days.

Solutions prepared with 4 pounds of 3,5-dinitro-o-cresol, 1 percent of commercial soap preparation, and 5 percent of blackstrap molasses in 100 gallons of solution killed adults of *Anastrepha ludens* in an average of 1.34 days at 77° F. The same concentration killed in 1.68 days after sprayed plates were held for 8 days at 77° F. and 50 percent relative humidity, and in 1.69 days after they were held for 28 days under the same conditions. The mean length of life was 1.51 days when a concentration of approximately 8 pounds of 3,5-dinitro-o-cresol was used in 100 gallons of solution containing 5 percent of blackstrap
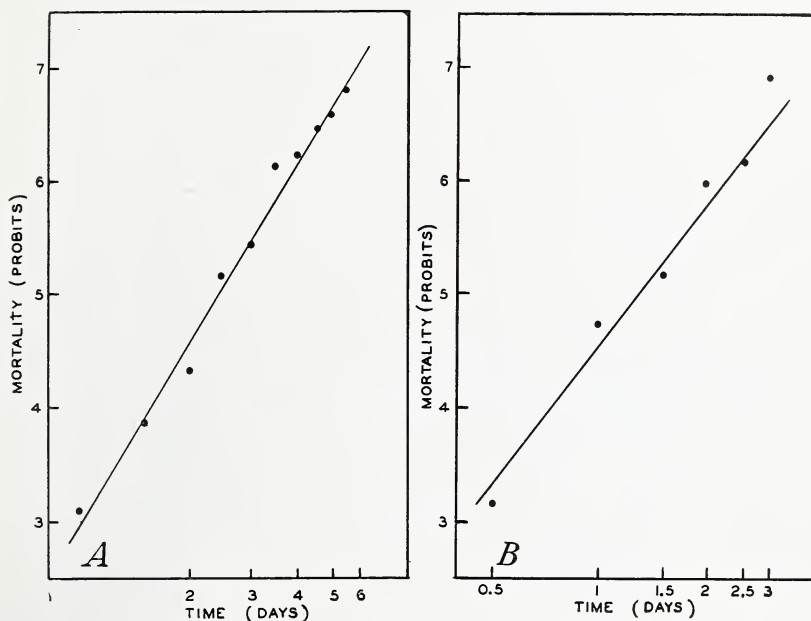
FIGURE 52.—Mortality of adults of *Anastrepha ludens* from the use of the following materials in 100 gallons of sprays: *A*, 4 pounds of cryolite with 20 pounds of sugar; *B*, 4 pounds of 3,5-dinitro-o-cresol with 1 percent of commercial soap preparation and 5 percent of blackstrap molasses.

molasses. The toxicity curve for the first three tests with 3,5-dinitro-o-cresol is shown in figure 52, *B*. More detailed studies on this compound will be reported at a later date.

Numerous other materials used in Plummer's preliminary tests gave low mortality. These were dinitronaphthalene, m-nitroaniline, diphenylguanidine, phenyl salicylate, thymol, diphenyl oxide, p-nitro-aniline, 2,5 dichloroaniline, 2,4, dinitrochlorobenzene, furacrolein, cre-sotinic acid, diphenylethylene, diphenylamine, diphenyl urea, benzoni-trile, phenothiazin, hexylresorcinol, theobromine, oxyquinoline sulfate, and lead antimonate.

From very early times the Indians in Mexico used preparations of the plant *Haplophyton cimicidum* A. DC. for killing cockroaches and other insects, and during the campaign against *Anastrepha ludens* carried on in 1900–1901 by the Mexican Commission of Parasitology

(*21, pp. 21, 28–30, 170, 195*) the use of sweetened extracts of this plant was truly extensive. At that time it was growing in abundance in the mountains of Morelos.

Because of its early use Plummer undertook a study of the plant with two objectives in view, (1) to determine the toxicity of samples from different localities and (2) to isolate if possible the active principle, so that the chemists of the Department might study its composition and possible synthesis. His report on these studies (*33*) included the information that had been obtained in his experimental work and results from the published information then available.

The toxic effect of decoctions of the leaves and stems when fed in
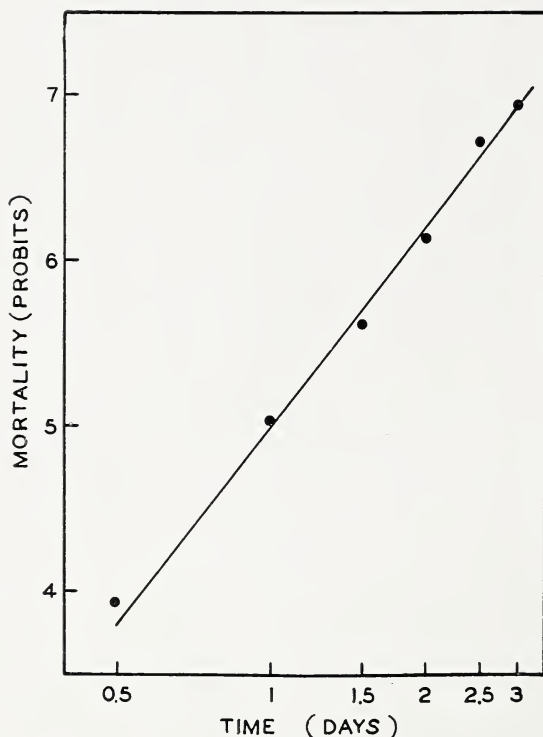
FIGURE 53.—Incapacitation including mortality of adults of *Anastrepha ludens* from extracts of *Haplophyton cimicidum*. (Data from Plummer (*33*).)

sirup mixture is to produce a type of paralysis which is followed at longer or shorter intervals by death. Since both the rate of paralysis and the death rate are important in measuring the efficiency of the poison and since the two combined constitute the best measure of that efficiency, the combined data on paralysis and mortality for the three runs available are shown in figure 53. While there was some irregularity in mortality or irregularity in paralysis, the combined data give a fairly consistent regression. These experiments were run at 77° F. and 60-percent relative humidity, with 22.7 gm. of leaves for 100 cc. of extract and with 18 percent of molasses. The influence of paralysis on the regression line shown may be gathered from figure 54, which shows the curves for paralysis and for mortality.

Experiments showed that aqueous extracts of the plant were not toxic after they had been held for 1½ years, but extracts with molasses sprayed on glass plates and allowed to dry retained their toxicity in this form for many months.

Although suitable samples of the plant gave extracts that were highly toxic, it was found that samples from different places or taken at different times varied in this respect. Some of them were of exceedingly low toxicity. This fact, coupled with the present relative
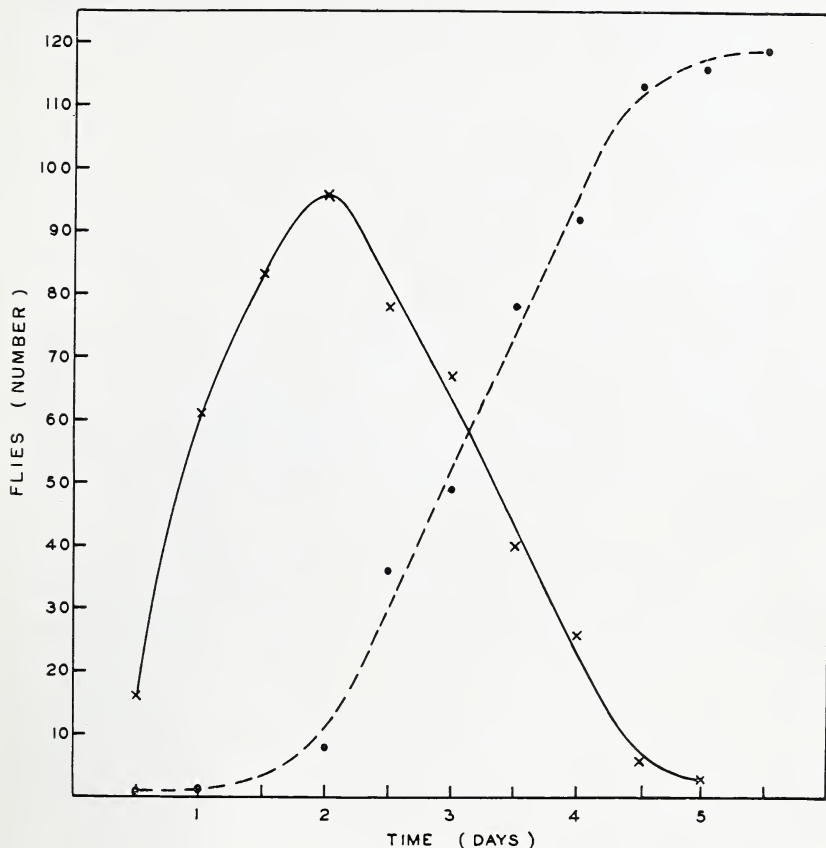
FIGURE 54.—Paralysis and mortality of adults of *Anastrepha ludens* from extracts of *Haplophyton cimicidum*. Solid line represents paralyzed flies and broken line represents dead flies. (Data from Plummer (*33*).)

scarcity of the plant, indicated that the most logical procedure was to obtain the active principle in the hope of producing it synthetically.

Studies made in the chemical laboratory succeeded in isolating materials which were nontoxic, but no crystalline toxic material was obtained. The toxic material appeared as a gummy substance in very small quantities, indicating it to be highly potent, but efforts to carry the work farther were unsuccessful. The studies made, however, appeared to indicate that the toxic principle is similar to that of an alkaloid in the methods by which it may be obtained, but apparently different in properties from the better known alkaloids.

When his work with other materials had been completed, and when indications appeared that tartar emetic would not alter fruit ratios, Plummer undertook a thorough study of the toxicity of this material. He conducted laboratory work under different controlled conditions and carried the work into the field on spray plots. His laboratory results were based on many tests with a total of over 6,000 flies.

Figure 55, E, represents a summation from his laboratory data in which a random 16 tests were used, the 40 flies of each test being equally divided as to sex. The results were very promising. However, they were obtained with 8 pounds of tartar emetic and 4 percent of sirup as opposed to 4 pounds of tartar emetic and 10 percent of sirup as used in preliminary tests by Baker. Plummer continued laboratory work with large numbers, using 4 pounds and 5 percent of molasses, and this dosage was taken to the field for early test in citrus plots. Tartar emetic, 4 pounds per 100 gallons of solution containing 4 percent of blackstrap molasses in 16 runs at 77° F. killed in an average of 2.89 days. Results from a test with 20 pounds of granulated sugar in 100 gallons in which 164 flies were used is shown in figure 55, C and F, for comparison with results from a similar test with sodium fluosilicate.

An example of the results from the different dosages of tartar emetic is shown in figure 55, A, B, and D, the curves being based on approximately 240 flies in each case. It is not known why the change in the higher mortalities is evident with 1 pound and 3 pounds, whereas 5 pounds gives a consistent mortality throughout. Work of this kind, however, indicated the possibility of using a lower dosage than 4 pounds, and some field plots were laid out on the basis of the use of 3 pounds.

Field results indicated the importance of developing a sticker, and work was undertaken [28] with glue, casein, caseinates, bentonite, and fish oil. Glue was used because it had been found that the flies fed greedily upon it in the laboratory. Tests were also run with reduced quantities of tartar emetic, with sodium fluosilicate, with barium tartrate, and with antimony oxychloride and antimony trioxde.

Work with fluorine compounds had been developed extensively in Florida during the campaign against the Mediterranean fruitfly, old compounds and new ones having been used in tests there and sprayed repeatedly in foliage tests. Foliage injury resulted in practically all cases, and for this reason it was not thought wise to recommend the fluorine compounds.

It seemed advisable, however, to test certain of these against *Anastrepha ludens*, since conditions of their use for the Mexican fruitfly might be different from those for *Ceratitis capitata*. In this connection figures 52, A and 55 F, may be compared, showing as they do results with cryolite and sodium fluosilicate. The population represented for drawing the curves was 238 for the cryolite and 160 for the sodium fluosilicate. The slightly better showing for the sodium fluosilicate therefore may be due in part to the numbers. Although cryolite looked promising in these laboratory tests, it appeared to give no reduction in the field, and therefore sodium fluosilicate was checked against it.

The field work with tartar emetic as well as that with other materials was conducted at Hacienda Santa Engracia on spray plots of grape-

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[28] See manuscript report 80, p. 154.

fruit and orange.[29]   The plan adopted was to record trap catches in the control plots and, after each spraying in the sprayed plots, to determine the reduction in population that was brought about by the spraying.   The formula used was 4 pounds of tartar emetic and 5 percent of molasses in 100 gallons of solution.   The work was handled by Plummer.
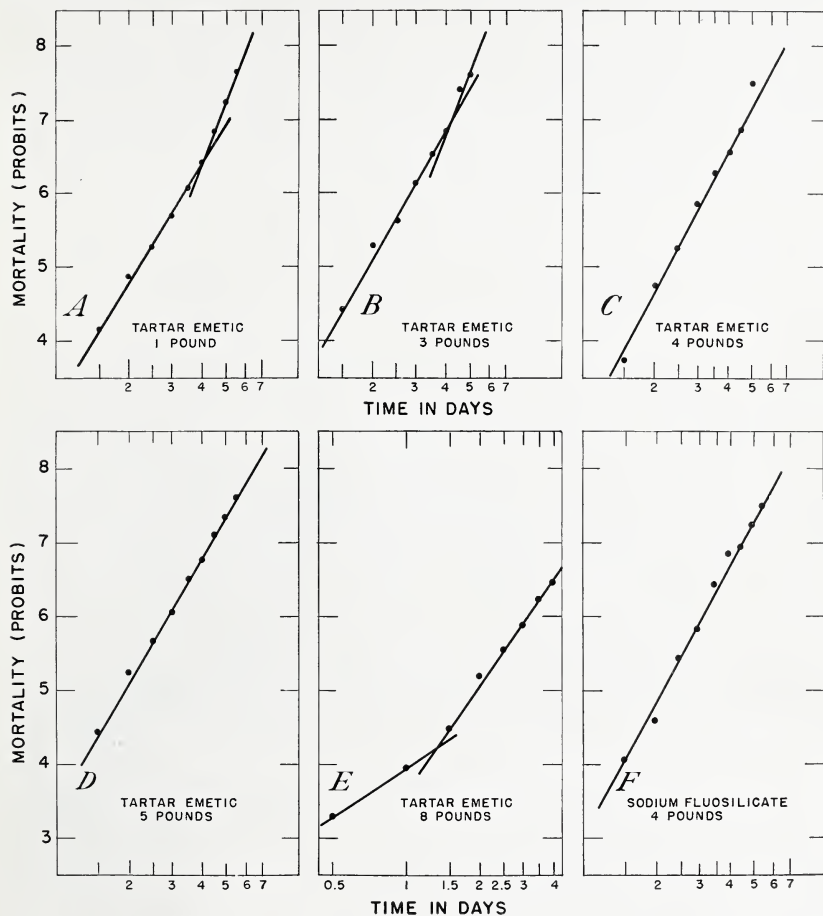
FIGURE 55.—Mortality of adults of *Anastrepha ludens* at 77° F. on plates sprayed with the following materials: *A*, Tartar emetic, 1 pound; *B*, tartar emetic, 3 pounds; *C*, tartar emetic, 4 pounds; *D*, tartar emetic, 5 pounds; *E*, tartar emetic, 8 pounds; *F*, sodium fluosilicate, 4 pounds.   All in water to make 100 gallons and with 20 pounds of granulated sugar, except in *E*, in which 4 percent of molasses was substituted.

The first spraying of grapefruit in the fall was made October 14, 1936.   Trap records were made from October 15–20, 20–25, and 25–30. On October 25 there was rain although none before that.   The reductions in population shown by the three trap periods were 91, 87, and 79 percent, respectively.   This indicated that the spray was really effective in the absence of rain.

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[29] See manuscript report 75, p. 154.

This may be compared with spraying on November 3, 13, 16, and 25, and December 5. It rained on November 8, 9, 10, 14, 16, 18, 19, 25, and 30. Population reductions for the periods after each spraying were 75, 32, 0, 0, and 23 percent, respectively. These figures plainly show the effects of these successive rains. Subsequently there was a period of 2 weeks without rain, when the reductions rose again to 74 and 86 percent, respectively.

A tartar emetic spray plot was laid out in January 1936, the first spray being applied January 21. This plot was composed of young oranges in which the fruitfly population was not very large. Figure 56 from Plummer's results [30] compares the populations in the spray plot
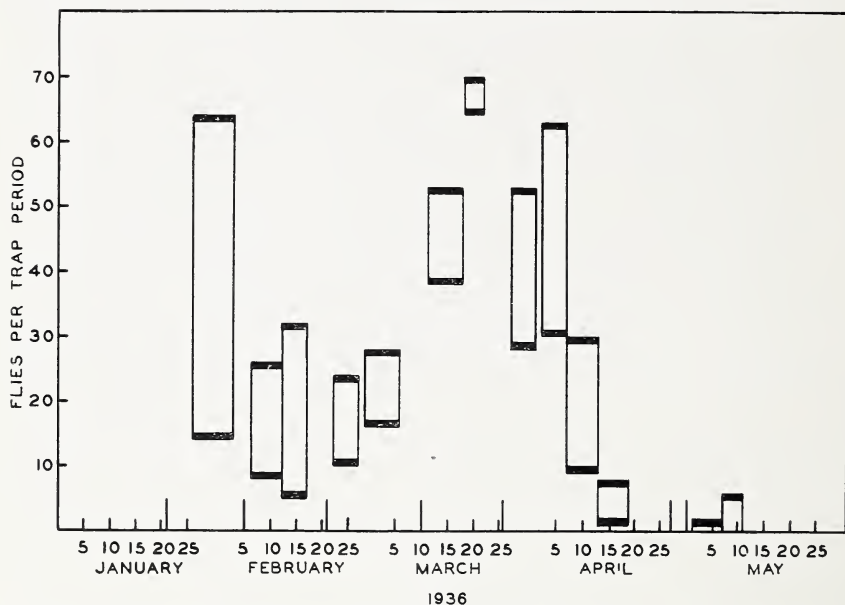
FIGURE 56.—Reduction of populations of adults of *Anastrepha ludens* in a plot of young oranges at Santa Engracia due to spraying with tartar emetic. The upper horizontal line represents numbers captured in 24 traps in the control plot and the lower horizontal line the numbers in 24 traps in the sprayed plot. The longer vertical lines at the bottom of the figure indicate the dates of spray applications.

and the control plot. The definite reduction following the first spraying will be noted in the figure. It will be noted also that the sprays on February 21 and March 10 did not succeed in holding down the population in the sprayed plot. There was rain on March 1, 2, 5, 6, 8, and 12. These rains were not heavy, but it appears that they were sufficient to reduce the effectiveness of the sprays applied February 21 and March 10. The population in the spray plot built up to almost that in the control plot.

Following March 12, there was no rain until about the end of the month, and the spray applied on March 26 is plainly reflected in the reduced populations during the periods directly following it. The reduction during the trap period immediately following maintained

[30] See manuscript report 66, p. 154.

itself with only a perceptible rise with the rising peak of populations during the first week in April, and the ratio was fairly held during the second week in April. Two sprays were applied at the end of April because the first application was washed off by rain the same day it was made.

On this plot, the first four sprays contained 5 percent of blackstrap molasses; the last three, 20 pounds of granulated sugar instead. All contained 4 pounds of tartar emetic to 100 gallons of solution. This plot sprayed during the winter season gives evidence that the tartar emetic will reduce fly populations under these conditions. What the picture would have been in March, if the weather had remained completely dry, it is difficult to say, but it is evident that after a population is built up it requires some time to reduce it. It is perhaps worthy of note that with small plots located in a generally infested region there is always a drift into the plots.

Work under way with reduced dosages of tartar emetic and the field trials with sodium fluosilicate for comparison with the results on cryolite have not reached a stage permitting conclusions.

Parasites and Diseases of Adults

No effort has been made to study the diseased conditions of adults. In some cases considerable numbers of flies can be found that turn a distinct red color. What the causes of this may be is not known. A great many abnormalities occur, one of which is the amputation of the ovipositor sheath, as mentioned on page 76. That intestinal disturbances occur is indicated by occasional abnormal conditions of the feces. But no epidemics causing high mortality have come to the attention of the authors, with the exception of those due to a species of fungi.

In the stock populations of Mexican *Anastrepha mombinpraeoptans* maintained in the laboratory very high mortality occurred in one instance which bid fair to eliminate the stock altogether. On a study of the flies Baker [31] found them to be attacked by a fungus reproducing asexually by globular, nippled conidia which formed on the tips of the branches of the mycelium. Sexual reproduction was not observed. The growth appeared as white masses between the segments of the abdomen some time before death, and the spread from fly to fly and from cage to cage was rapid. To prevent complete loss of the stocks, Stone removed all flies from the rearing room, and this was thoroughly cleaned with formalin. The remaining flies which appeared uninfected were removed to cages that had been cleaned in the same way and dried in the bright sun. The flies were held for a time in a second room before they were returned to the stockroom. No further difficulty developed.

This occurrence, however, suggested the possibility of the presence in nature of a parasitic organism that might perhaps be utilized. A search was therefore regularly made of field material in different localities. An occasional infected fly was discovered, but there appeared to be no general occurrence of the disease anywhere at any time. It seems probable, therefore, that conditions suitable to its development to epidemic proportions, while present at the time in the

[31] See manuscript report 52, p. 153.

rearing quarters, did not occur in the field, and that under natural conditions the causative organism would make little progress and its artificial use as a controlling agent would not be indicated. It is one of those fungi belonging to the Entomophthorales.

Another type of fungus was noted rather frequently. Several species occur and they attack not only *Anastrepha ludens* but the other common species of *Anastrepha* as well. Any part of the body may be attacked, even the mouth parts, and the parasites may be seen in groups forming tufts protruding from the part attacked. While the several species differ in form, they appear to be similar in biology. Baker worked out the life cycle of one of the commoner species.

The thallus in this case is attached to the fly by a heavy, slightly curved hook and is composed of a slender shaft, a swollen cylindrical body above it which is followed by a constricted neck, and a lobed tip at first plainly conical, no doubt the trichogyne. From the top of the shaft a branched structure extends to the side, terminating in numerous nipple- or flask-shaped antheridia. Issuing from these may be seen minute, spherical, highly refractile, nonciliated bodies which may be located again within the neck of the structure previously mentioned. In this main body the two-celled, spindle-shaped, slightly curved spores develop. Each spore gradually becomes thickened at one end, which on touching the body of the fly adheres and the developing hook takes hold. The main features are shown in figure 57.

While these fungi are picturesque and interesting in their complicated reproductive structures, they cause little inconvenience. Flies may be seen with tufts of them attached to their abdomens, legs, antennae, or mouth parts going about unconcerned. The fungi appear never to wipe out populations as does the fungus previously described, and they may therefore be considered as of no great economic importance. They belong to the order of Laboulbeniales, a group which apparently has not been very completely studied. The species attacking the fruitflies seem to be undescribed.

Very seldom are animal parasites observed attacking the adults. Occasionally flies may be found covered with mites. These are at times so thick on the wings as to touch one another. No special study has been made of them, since their occurrence is infrequent, and for this reason alone they would not be of economic importance so far as the flies are concerned.

SURVEYS

From time to time during earlier years American entomologists have visited Mexico to obtain knowledge regarding fruitflies, especially *Anastrepha ludens*. Brief reference will be made here, however, only to those field excursions made by individuals in connection with the present project, i.e., the Mexican laboratory of the Bureau of Entomology and Plant Quarantine of the United States Department of Agriculture.

In 1927, as a preliminary to the organization of the laboratory, Zetek [32] and Baker made a survey as far south as Morelos, spending considerable time in that State. Zetek covered alone the territory from the lower part of the Nuevo León citrus district down to the Tampico area. At that time Hacienda Santa Engracia, where infes-

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[32] See manuscript report 4, p. 152.

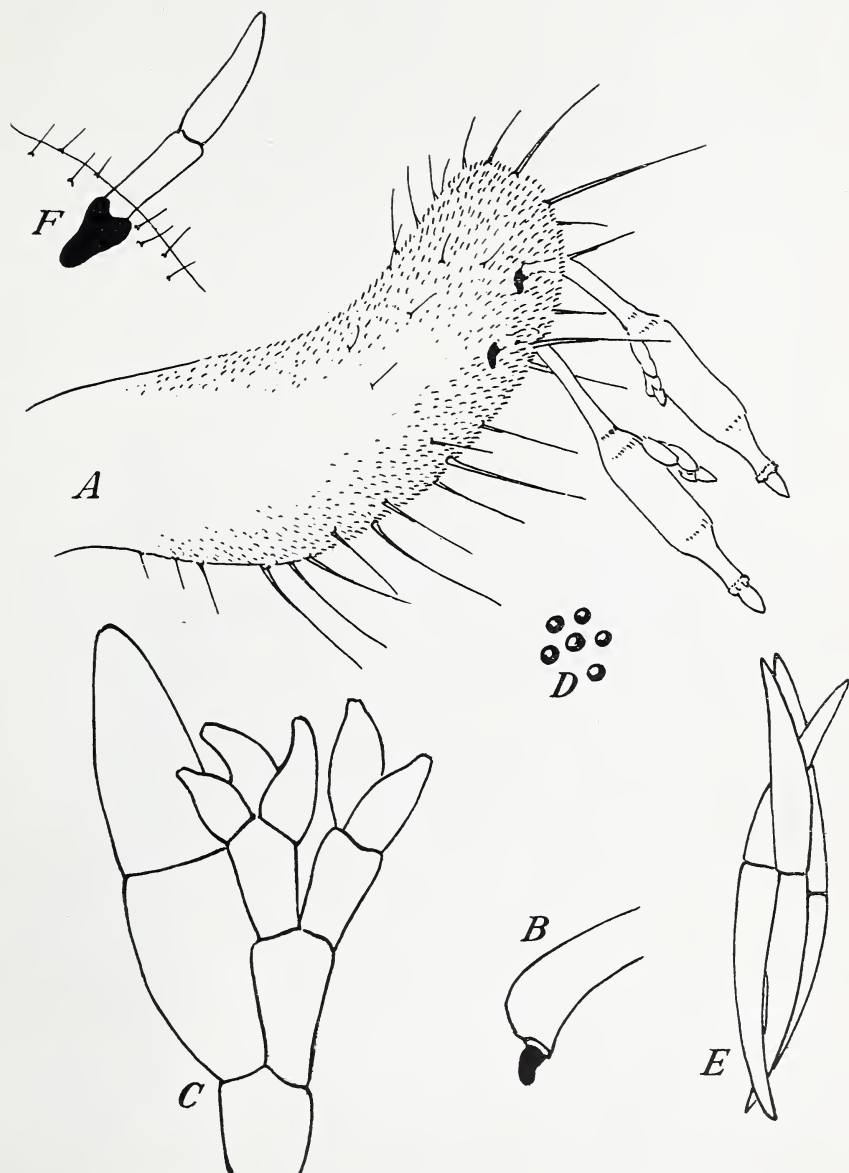FIGURE 57.—Details of a fungus commonly attacking adults of *Anastrepha ludens:* *A*, Palpus of *A. ludens*, showing fungus bodies attached; *B*, tip of one of these bodies, showing the hook used for attachment; *C*, young fungus, showing structure; *D*, refractile bodies that emerge from the antheridium; *E*, mature spores; *F*, a spore after attachment, showing the formation of the anchoring hook.

tations are now heavy and where field work is now being conducted, was visited; but infestation was considered so light at the time as not to warrant work there. At approximately the same time Baker studied the territory forming a belt east and west, south of the Rio Grande, giving special attention to wild fruits, but was unable to locate infestation in any of the native fruits in the region visited.

The following year permanent work was started in Morelos and in Mexico City, and the area about Veracruz was visited by Molino and Baker, Molino swinging in through the region of Jalapa.

Skwarra, who was especially engaged for survey work, began study in the State of Morelos, and made her first extended trip through the State of Oaxaca in October and November 1928,[33] beginning at Teotitlán. Here she found 21 kinds of fruits in cultivation, but according to her report none were shipped from the region, since the fruits are so heavily infested that the packing houses do not buy them. Even the local production of citrus she found to be hampered, and she mentioned that oranges are shipped into the region.

Her second journey was to the States of Michoacán, Jalisco, and Nayarit during December 1928. Infestation of oranges was recorded in Uruapan, Michoacán. In San Andrés, Jalisco, infestation was evident in the fallen oranges, as well as in other fruits. She was unable at that time to find any infestation in Tepic, Nayarit.

In 1929 Skwarra made a study of the fruit region of Veracruz.[34] Here there is extensive citrus production, and, while she found infestation in many places in cultivated fruits of various kinds, at no place did she record wild native fruits as infested. The carry-over was from one kind of fruit to another in the gardens. More recently Stone and Plummer [35] made visits to the Cordoba region, studying infestation there.

Stone visited the Isthmus of Tehuantepec via Veracruz in 1932. Plummer also traversed that region in 1932, riding across from Chiapas to Tabasco, and Baker reached the Isthmus in 1933, riding over the mountains from Oaxaca. While *Anastrepha ludens* no doubt occurs, none was actually found on these trips. Returning, Stone traveled down the Jaltepec and Coatzacoalcos and up the Chalchijapan to Dos Ríos. In all the small villages oranges were growing, and mangoes, guavas, grapefruit, and sapotes were noted, but fruit itself was exceedingly scarce, and that examined was uninfested. According to the residents, all the guavas, which at the time were unavailable, are heavily infested, no doubt by *A. striata*, while the mangoes and oranges are less attacked. Evidently, however, the species involved in the latter cases is *A. ludens*.

Through the courtesy of President Walter Douglas, of the Southern Pacific Railway of Mexico, Baker [36] examined the west coast territory from the citrus plantings of Sonora south to Tepic. No infestation was found in Sonora, and apparently *Anastrepha ludens* has not yet reached that State, but by the time of this visit (1935) it had spread as far north on the west coast as Culiacán.

In Jalisco, Baker [37] visited especially the citrus regions of Atoto-

[33] See manuscript report 7, p. 152.
[34] See manuscript report 13, p. 152.
[35] See manuscript report 57, p. 154.
[36] See manuscript report 56, p. 154.
[37] See manuscript report 50, p. 153.

nilco, Ayo, and Tequila.[38]   The plantings in Atotonilco are in a beautiful isolated valley, and the infestation is light, since no larvae were found during the visit. At Ayo also the infestation is light, one infested fruit being found there. The situation in both these regions is in striking contrast to that at Tequila.   There in a citrus grove glass traps were hung in the morning, and by evening they had captured from 12 to 25 flies per trap, whereas during a day's exposure in Atotonilco no flies were captured in any traps.

The fruit regions near Mexico City have been frequently visited by members of the staff, as has the west coast in Oaxaca, and Baker traversed the central plateau area.   With the construction of the high-
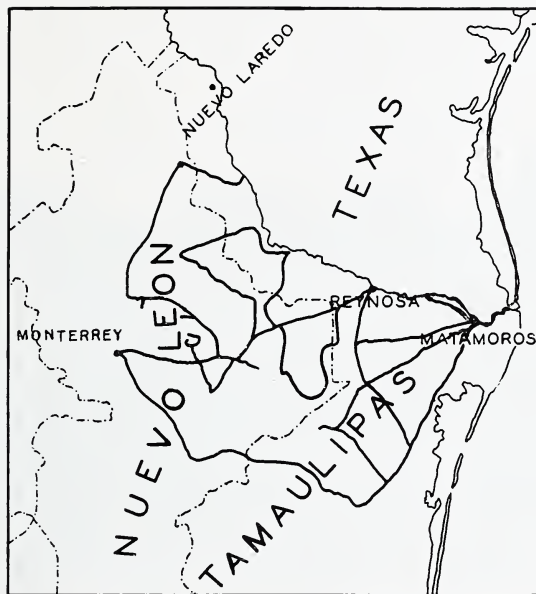

FIGURE 58.—Routes taken in Mexico by McPhail, Hensley, and Gingrass on a survey for *Sargentia greggii.*

way visits have been made along this route, but the peninsula of Yucatán has remained untouched by members of the laboratory staff.

The northeastern area, from the Rio Grande south, has been repeatedly examined, and recently McPhail,[39] together with H. S. Hensley and C. O. Gingrass, members of the force of the Division of Fruitfly Control in Texas, have scouted much of this territory for the presence of *Sargentia greggii.*   The routes taken are shown in figure 58.   An extensive growth of *Sargentia* was located near Cerralvo in the locality known as Plan de los Nogales y Carboneros.[40]   Here there was estimated to be about 1,000 acres of the plant.

[38] In his entomological observations in the west-coast territory, in Jalisco and in Veracruz, Baker had the collaboration of Dampf as representative of the Mexican Secretaría de Agricultura y Fomento, a collaboration of much benefit owing to the latter's knowledge of local conditions.   Throughout his tenure of office with the Mexican Secretaría Dampf showed a keen interest in the work, and other officials of that organization, both in Mexico City and in the various regions visited, have given assistance, all of which has greatly facilitated the survey work.   Among these De la Barreda, whose early studies on *Anastrepha ludens* have been cited, has been especially helpful.
[39] See manuscript report 79, p. 154.
[40] See manuscript report 78, p. 154.

The plant was located again along the banks of the Río de las Lermas about 2 miles east of Monterrey, and at that time, the middle of July, fruit infestation was found. *Sargentia* was also found growing on the road to Chipinque near Monterrey, Nuevo León. On a subsequent trip it was found at Garza González and was later found growing at Cruillas, El Milagro, Burgos, and Hacienda Guadalupe. At Hacienda Guadalupe the growth was extensive and was abundant following a stream at La Presa. At El Milagro it was well distributed throughout the area, occurring most abundantly near the bases of the mountain peaks and ridges. It occurs along the road south of Monterrey and grows extensively in and about Hacienda Santa Engracia. The *Sargentia* locations and rough distances from Rio Grande Valley citrus are as follows: Cerralvo, 80 miles; Garza González, 80 miles; Burgos, 95 miles; Cruillas, 100 miles; Hacienda Guadalupe, 120 miles; and Linares-Monterrey, 130 miles.

FIGURE 59.—Characteristic environment for *Sargentia greggii* on Hacienda Guadalupe, Mexico.

McPhail [41] has also scouted the river bottoms along the Rio Grande, but so far has not found *Sargentia* there.

A typical environment for *Sargentia* is shown in figure 59 taken on Hacienda Guadalupe. The tree, however, also occurs in much more scrubby growth than this. Sometimes it becomes very large (fig. 2) and very much resembles a citrus tree.

STUDIES OF OTHER SPECIES OF ECONOMIC IMPORTANCE

When the Bureau laboratory was established in 1928, work on the taxonomy, embryology, and anatomy of the Mexican fruitflies had been reserved by Dampf (*11*), as indicated in his address before the International Congress of Entomology. Taxonomic work at the laboratory, therefore, was not planned as a major project, but studies of immediate necessity in clearing up the laboratory material were undertaken by the senior author in 1931.

[41] See manuscript report 82, p. 154.

The studies referred to, based on the laboratory specimens, have resulted in the segregation of the Mexican material so far studied into 8 described species and 11 considered new to science. With the exception of *Anastrepha tripunctata* V. d. W. and *A. robusta* Greene, examples of which have not appeared in the laboratory material, the 19 Mexican forms have been dissected, figured, and segregated by the senior author by means of keys to permit their identification. Segregation in the adults has been made mainly on the structure of the claspers and ovipositors, the nature of the membrane armature, the character of the antennae, and the banding of the wings. In the larvae the chief reliance has been placed on the structure of the spiracles.

It was considered advisable to group the Mexican forms not into the one genus *Anastrepha* but into three genera, an action which would result in more compact groups structurally and biologically. Following the practice adopted by the senior author in his classification of the plant lice, habits were studied and structural characters looked for in that connection. Thus efforts were made to correlate the habits of species with their structure.

FIGURE 60.—Armature of the sheath membrane of *Pseudodacus pallens*.

PSEUDODACUS PALLENS Coq.

The first step was a study of the structure of *Anastrepha serpentina*, the type species, and of *A. ludens* and *A. striata*. With a knowledge of these forms in hand a detailed examination was made of examples of *Pseudodacus pallens* from material collected in Texas. *P. pallens*, at that time considered by taxonomists to be a typical *Anastrepha*, was found to diverge rather widely from the other three in structure of claspers, penis, armature of the sheath membrane (fig. 60), and ovipositor. The facts of these differences were ultimately recorded by drawings [42] and material of *P. pallens* from Texas was supplied to Dampf (*12*) for a publication on the ovipositors of members of the genus *Anastrepha* in which he treated the females under the designations *A. fraterculus, A. ludens, A. serpentina, A. striata*, and *A. pallens*.

The structure of *Pseudodacus pallens*, especially that of the ovipositor, led the senior author to the prediction that the larvae would

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[42] See manuscript reports 34 and 44, p. 153.

be found feeding in seeds or in some small berry, and that, in agreement with the adults, they would differ from larvae of *Anastrepha*. With the inauguration of the trapping system in the Rio Grande Valley *P. pallens* was taken in very large numbers in groves, and the possibility that it might be involved in fruit infestation arose. McPhail and Berry (*28*), the latter attached to the force of the Division of Fruitfly Control in Texas, began an intensive study in the Rio Grande Valley to determine the biology of the species. They succeeded in working out the life cycle and demonstrated that the larvae live in the seeds of a small fruit called "la coma" (*Bumelia spiniflora* A. DC.). The population of *P. pallens* in any year is dependent on the condition of the coma crop, and after the coma fruits have fallen the adults migrate for feeding purposes, in this way spreading into the groves. The species ranges through the lower portion of Texas and the northeastern part of Mexico. Since the opening of the work at Santa Engracia, it has been abundantly trapped and reared there. In all the extensive trapping in Morelos this fruitfly has not been taken there.

The completion of the story on *Pseudodacus pallens*, however, confirmed the opinion regarding its differences from members of the genus *Anastrepha*. The structures originally used for this differentiation had been those of the adults. The discovery of the larva proved it to be different from the larva of *A. serpentina*. For differentiation of the larvae in all species the senior author has used the size, number, and arrangement of the interspiracular processes, having found them to be dependable characters in this group. Figure 61, *A*, shows these processes in connection with the spiracles of *A. serpentina*. It will be seen that they are of moderate length and rather coarse. The spiracles in the figure are numbered, since the senior author selected spiracle No. 1 (i. e., the spiracle opposite the free group of processes) for comparison throughout different species. While there are four groups of processes to each spiracular plate, there are only three of the large associated glands below the body surface. The space opposite the free group of processes separates the spiracles rather widely, and this space, together with the occurrence of only three glands and three spiracles, suggests an earlier, more complete condition.

Figure 61, *B* and *C*, are given as confirmatory figures, since it has been repeatedly assumed that the larvae of fruitflies cannot be distinguished. *B* is the first spiracle of material from zapote mamey prepared in 1932. *C* is from chicozapote prepared in December 1937, both taken from populations at random. The similarity needs no comment.

Comparing with these the drawings in figure 62, which represent the spiracle of *Pseudodacus pallens*, it will be seen at once that in *P. pallens* the processes are greatly reduced in comparison with those of *Anastrepha serpentina*. They are on a small hump, are short, straight, and sometimes appear slightly clubbed. In some preparations the processes of *P. pallens* appear simple, very straight, and slightly bladelike. In others they are branched. Figure 62, *B*, shows a spiracle from a preparation where the cover slip in the mounting has spread the processes into a rosette. In this case the processes are branched.

In view of these facts the senior author suggested that *pallens* be removed to eliminate this species from consideration in *Anastrepha;*
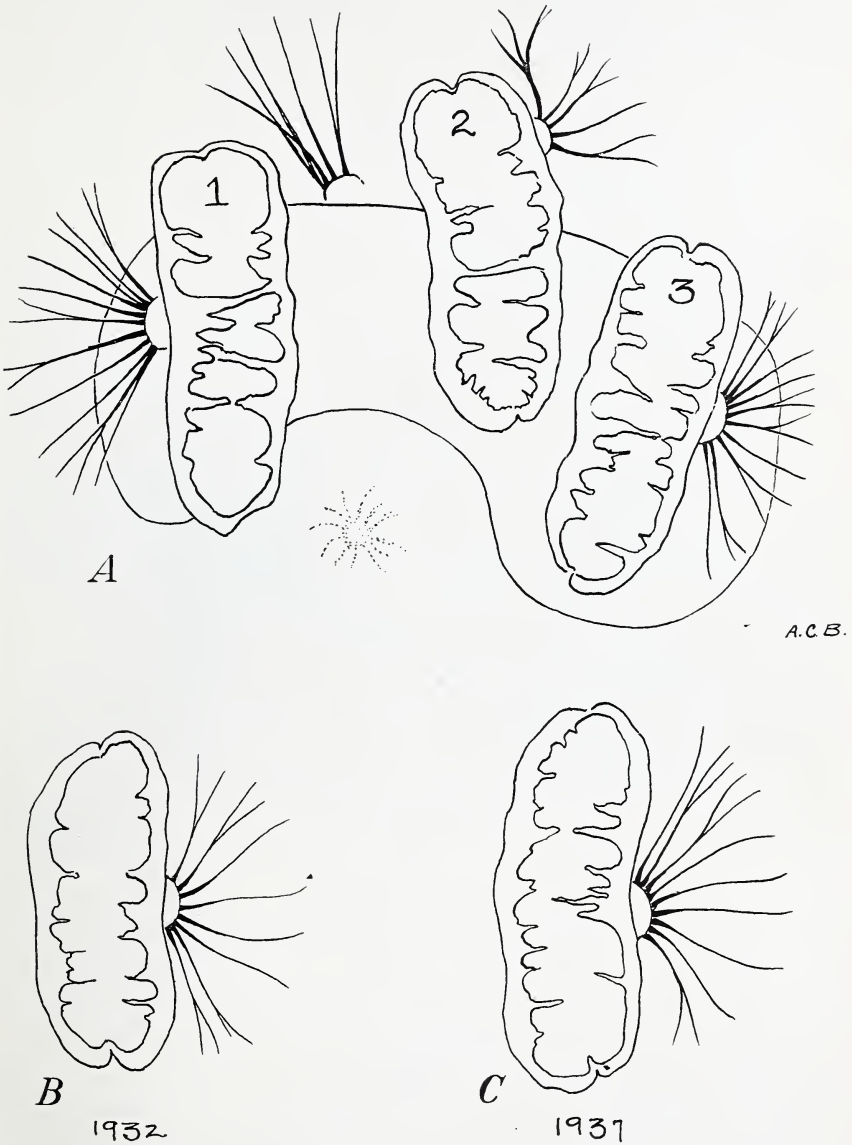
FIGURE 61.—Spiracles of larva of *Anastrepha serpentina*, showing interspiracular processes: *A*, Entire spiracular plate; *B*, first spiracle of larva taken in 1932 from zapote mamey; *C*, first spiracle of larva taken in 1937 from chicozapote.

and this was done by Alan Stone (*40*) in 1939. Another species, with a long, slender ovipositor sheath and a wing without cross bands, was at first represented by a single female taken in one of the traps at Cuernavaca. Subsequently other specimens have been trapped in Cuernavaca, and the species has since been described as *Pseudodacus bicolor* by Alan Stone (*40*).
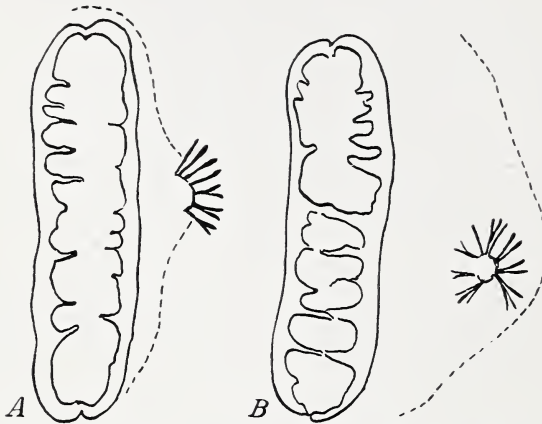

FIGURE 62.—First spiracle of larva of *Pseudodacus pallens*, showing interspiracular processes: *A*, In normal position; *B*, the processes as spread out by the cover slip in the mounting.

LUCUMAPHILA SAGITTATA Stone

Attention may now be directed to a species to which the senior author gave the manuscript name *sagittata*, and which was later described by Alan Stone (*39*). Its discussion is in keeping here, since it injures large numbers of yellow sapotes (*Lucuma salicifolia* H. B. K.), a fruit of considerable importance in Mexico.

In the early work of the Mexican Commission of Parasitology (*21, p. 80*) reference was made to giant adults of *Anastrepha ludens* occasionally found. Of the hundreds of thousands of specimens of *A. ludens* reared at the laboratory no such gigantism has been observed. However, a species roughly resembling *A. ludens*, and probably accounting for the idea, has been taken in numbers in Cuernavaca by the members of the laboratory staff, the first specimen by Plummer. This species possesses a dark band across the thorax much like that described for *A. robusta* Greene, but the ovipositor sheath is long and slender, not short and broad as is that of *A. robusta*.

The species differs distinctly from those of *Anastrepha*. The hooks of the ovipositor membrane are reduced to small scales throughout (fig. 63, *A*). Figure 63, *B*, also shows what the senior author has termed the mouth tube. The ovipositor itself is long and exceedingly slender and is armed with a barbed head like an arrow. The tip of the ovipositor is shown in figure 64; and in view of the fact that the fly is a very large one, much larger than any of the species of *Anastrepha* herein discussed, the comparison of this figure with those of the ovipositor tips of the other species will at once show the striking

differences. The claspers of the male (fig. 65, *A*) are small, rather rounded, suggesting those of *Pseudodacus pallens* (fig. 65, *B*), and have teeth near the tip. These characters led the senior author to segregate this form also from *Anastrepha* and tentatively to place it in a new genus which has since been described as *Lucumaphila* by Alan Stone (*39*). The structure of the ovipositor also permitted the prediction, made as soon as the adults were studied, that the larvae would be found feeding in seeds.

Some years passed, however, before the life cycle of the species was established. W. E. Stone, finding the larvae of a large trypetid feeding in the seeds of the yellow sapote, suspected that he might have discovered the larva of *Lucumaphila sagittata*. Rearings confirmed
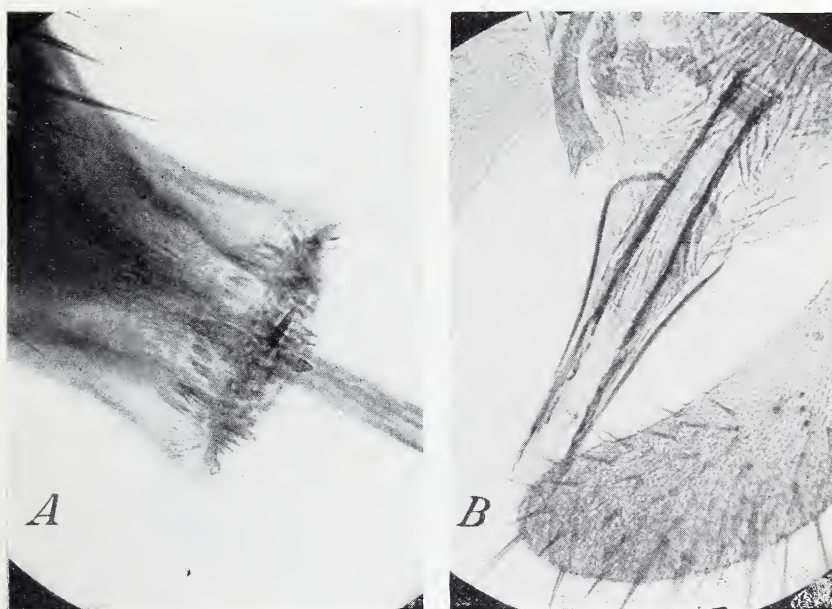

FIGURE 63.—Photomicrographic details of structures of *Lucumaphila sagittata:*
A, Armature of ovipositor membrane; *B*, mouth tube.

this suspicion. The larvae are about the size of those of the papaya fruitfly (*Toxotrypana curvicauda* Gerst.), 13 mm. in length. According to Stone's study, the period in the puparium requires 32 to 33 days at 77° F., whereas *Anastrepha ludens* under similar circumstances requires only 18 to 22 days. The larva feeds in the seeds, and after it matures it burrows from the fruit, leaving a characteristic exit hole (fig. 66, *A*). The channel through the pulp of the fruit (fig. 66, *B*) ruins it. Stone found 111 yellow sapotes infested out of 168 purchased in the markets of Mexico City. Incidentally, he discovered that the yellow sapote may serve for double infestation, *L. sagittata* feeding in the seed and *A. serpentina* feeding in the pulp. When this work was under way it was recalled that Skwarra had found what she thought was the papaya fruitfly feeding in yellow sapote, although the adult was not reared. Her record is evidently the first for the larva of *L. sagittata*.

FIGURE 64.—Tip of ovipositor of *Lucumaphila sagittata*, showing sensoria and structure of apex.
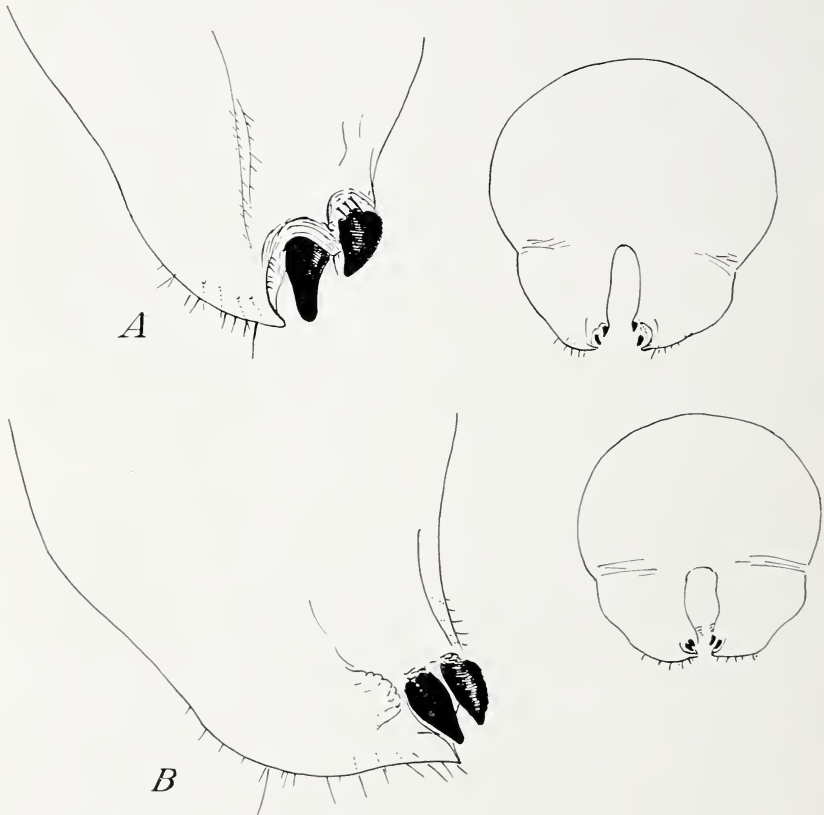

FIGURE 65.—Male claspers showing character and location of the teeth: *A,* Of *Lucumaphila sagittata; B,* of *Pseudodacus pallens.*
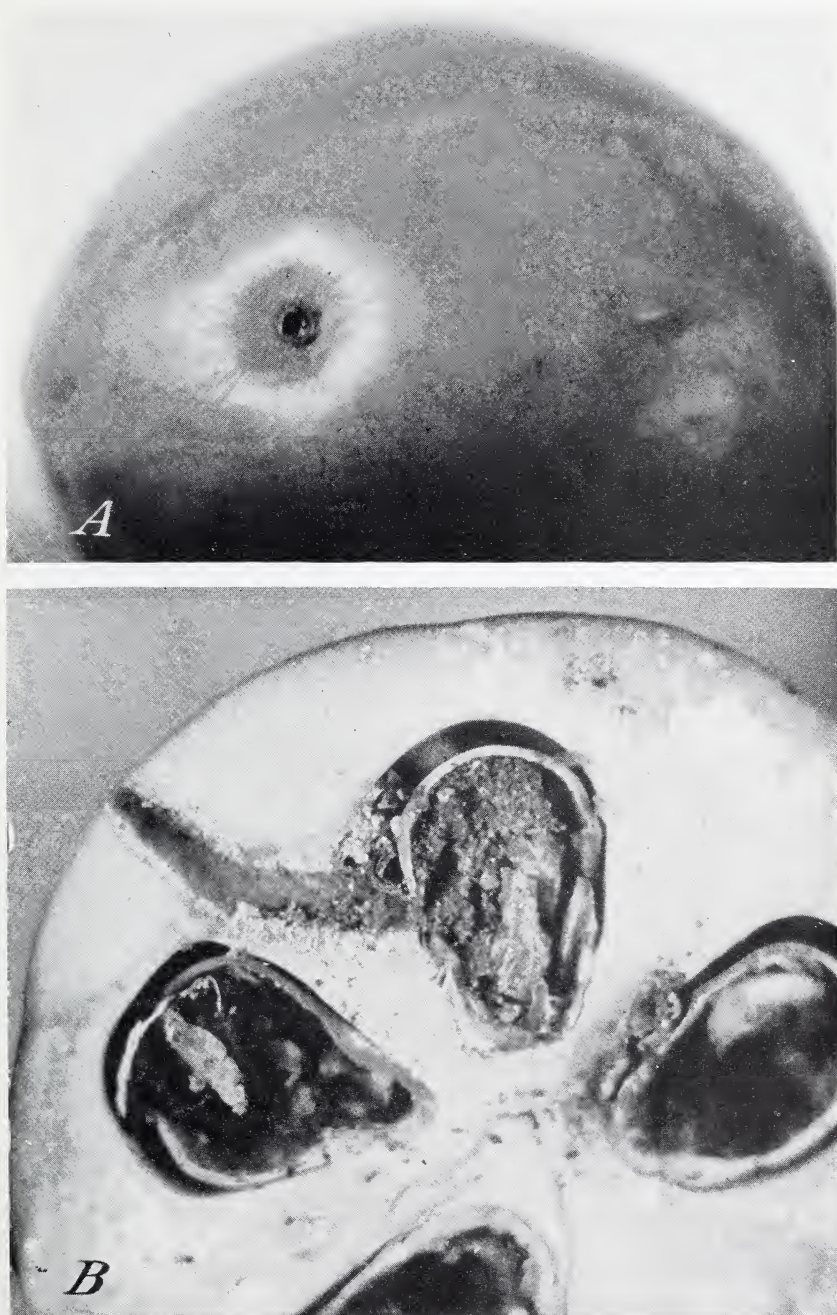
FIGURE 66.—Injury to yellow sapote by larvae of *Lucumaphila sagittata: A*, Exit hole of larva ; *B*, injury to seed and pulp.

The discovery of the larva and of its habits confirmed the segregation made on the basis of the adult. Figure 67, *A*, represents the first spiracle and figure 67, *B*, a mouth hook. The spiracular processes are exceedingly reduced and are located on a thickening as in *Pseudodacus pallens*. The segregation of *Lucumaphila sagittata* was supported also by the examination of a male of *L. obscura* (Aldrich), which appeared in every way similar, and by the discovery, on a trip to Jalisco by Dampf and the senior author, of a second new Mexican species which has been described as *Lucumaphila dentata* by Alan Stone (*39*). This form had been carried under the name *dentata*.
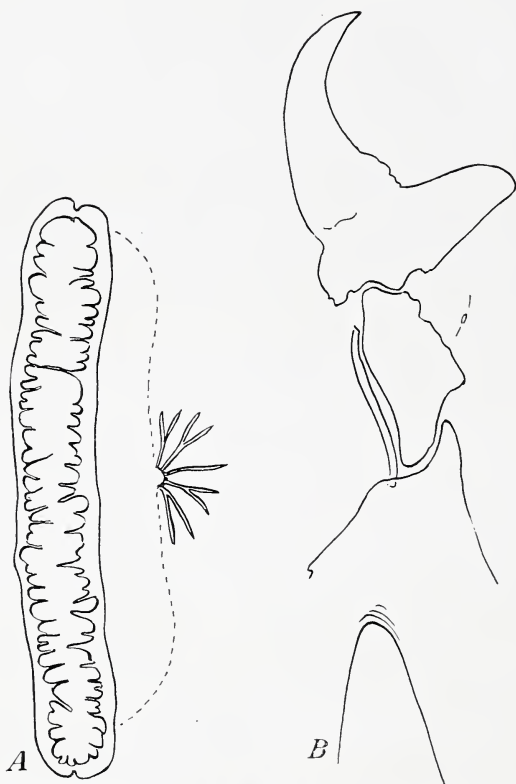
FIGURE 67.—Structures of *Lucumaphila sagittata: A*, First spiracle of larva, showing interspiracular processes; *B*, mouth hook of larva and its articulation.

According to a personal communication from Alan Stone the female of *L. obscura* also possesses a barbed tip to the ovipositor, as do *L. sagittata* and *L. dentata*. The existence of a generic group composed of species like *L. sagittata* and probably associated with *Lucuma* is therefore evident.

CHARACTERISTICS OF THE OVIPOSITOR OF ANASTREPHA

If the species related to *Pseudodacus pallens* and those related to *Lucumaphila sagittata* are removed, the remaining Mexican fruitflies in the genus *Anastrepha* form a fairly compact group as to structure

and, so far as known, as to biology. It will be unnecessary here to discuss the new species segregated by the senior author except insofar as their biology is important or insofar as they have been confused with species of economic importance. Certain species therefore will receive no mention. Insofar as he has accepted them, all have been described by Alan Stone (*41*) in a recent revision of the genus.

An idea of the sensory structures of the ovipositor, however, is important. At the beginning of the work in Mexico, Dampf pointed out the diagnostic value of the serrations of the ovipositor tip. Baker extended the method of diagnosis to include the character of the sensoria, and these structures have been employed since that time. Figure 68, *A*, represents the ovipositor tip of a female of Mexican *Ana-*
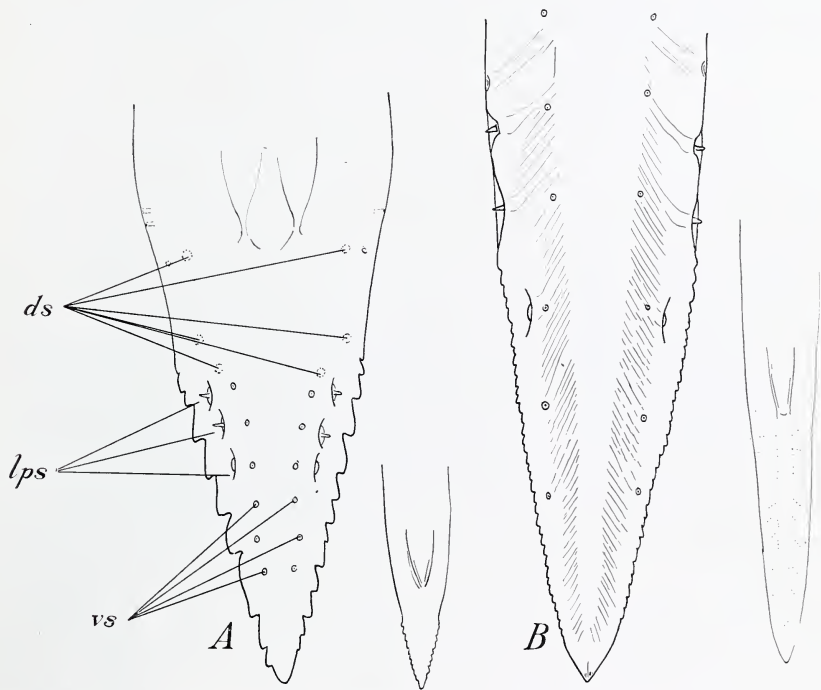
FIGURE 68.—Ovipositor tips of fruitflies, showing the marginal serrations and arrangement of sensoria: *A*, Mexican *Anastrepha mombinpraeoptans; B, Toxotrypana* sp. The letters in *A* designate the dorsal sensoria (*ds*), the lateral pit pegs (*lps*), and the ventral sensoria (*vs.*).

strepha mombinpraeoptans. The important sensoria for topographical purposes are the three groups of lateral pit pegs (*lps*). These are in the median plane. The most distal pair is characteristically without a peg. In some species (*A. passiflorae* Greene) this peg becomes quite prominent. The ventral sensoria (*vs*) are arranged in two rows on the toothed blade whereas the dorsal sensoria (*ds*) are on the basal part proximad of the toothed blade. In Mexican *A. mombinpraeoptans* there are typically six pairs of ventral sensoria on the blade. The position of the peg sensoria in relation to the teeth of the blade and in relation to the ventral sensoria, as well as the shape and dentition of the ovipositor blade itself, is of diagnostic value.

Even if the ovipositor varies greatly in shape, the six pits and the four pegs orient the rest of the structures on the blade. Figure 69, *A*, represents the ovipositor tip of a Mexican species of *Anastrepha* to which the senior author had given the manuscript name *A. spatulata* (see Stone, *41*). Here the pegs are long and slender, but the six characteristic pits are present and, because of the broadness of the ovipositor, their location forms the margin of a sort of differentiated area.

Even where the blade of the ovipositor becomes so broken into several lobes that the organ is entirely different in appearance and probably in manipulation, as it is in figure 69, *B*, the two pairs of pegs remain to orient the observer. The lobed ovipositor figured is that of a species in a closely related genus which causes heavy damage to mulberry twigs in Morelos.

FIGURE 69.—Ovipositor tips of Mexican species of fruitflies: *A, Anastrepha spatulata*, showing the prominent nature of the pit-peg sensoria; *B*, a species closely related to those of *Anastrepha*, showing location of sensoria on a greatly modified ovipositor.

The ovipositor of *Lucumaphila sagittata* is long and exceedingly slender. The sensoria at the tip (fig. 64) are arranged in an even row. Those that correspond to the pegs appear to be in the center. Old flies are commonly found in which the point is rounded like that illustrated, almost as if worn.

In the genus *Toxotrypana*, which in some ways is closer to *Anastrepha* than to forms like *Lucumaphila sagittata*, the tip of the ovipositor which forms the blade is flattened. As will be seen in figure 68, *B*, the two pits without pegs are in the toothed blade, but the two pairs of pits for the lateral pegs are crowded to the very edge of the ovipositor. Nevertheless, they are characteristically like those of the genus *Anastrepha*. With these peg sensoria as a source of reference, the sensoria on the ovipositor tip of any species may be clearly placed and their diagnostic value utilized.

It seems evident that the group containing the species closely re-

lated to *Pseudodacus pallens* has its affinities with the group containing species closely related to *Lucumaphila sagittata*, and that neither group could be confused with *Anastrepha*. This is evident from the similarity of the spiracles of the larvae (figs. 62, *A*, and 67, *A*), the similarity of the claspers (fig. 65, *A* and *B*), the long needlelike ovipositors, and the seed-feeding habit.

ANASTREPHA SERPENTINA Wied.

Attention may now be turned to the type of the genus, *Anastrepha serpentina*. The species is very beautifully marked as to body and
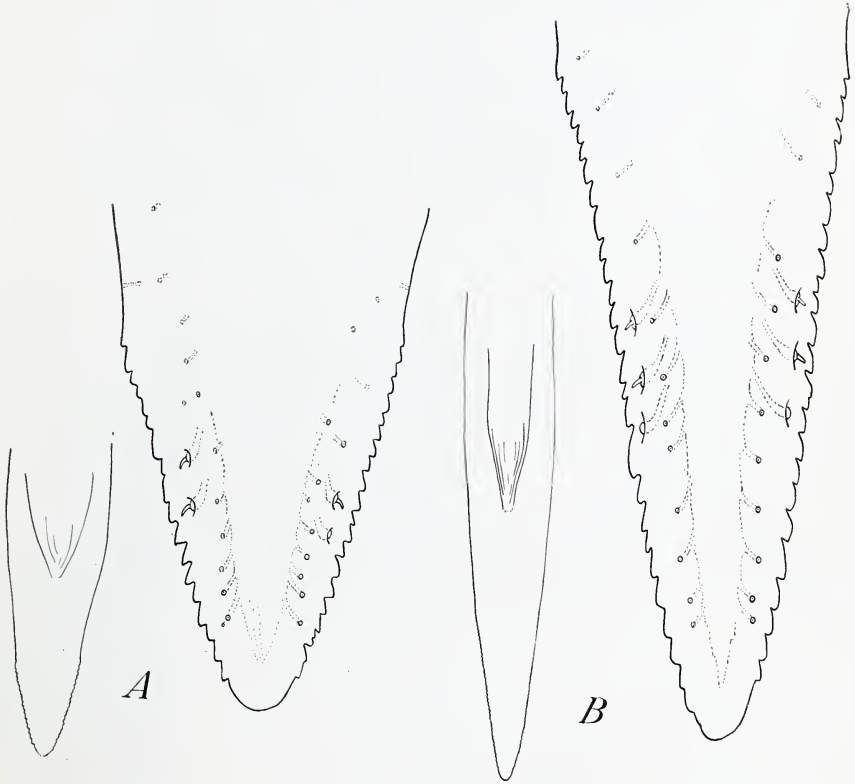
FIGURE 70.—Ovipositor tips of closely related species of fruitflies: *A*, A new Mexican form close to *Anastrepha serpentina; B*, ovipositor tip of *A. serpentina*, showing the marginal teeth and arrangement of sensoria.

wings, and it could in no way be confused with other members of the genus were it not for the fact that there appear to exist in Mexico other species of practically the same color pattern. The ovipositor tip of one such form is represented in figure 70, *A*. Compared to that of *A. serpentina* shown in figure 70, *B*, it is short and broad and the ovipositor opening is much nearer the tip. It will be noted that with *A. serpentina* the peg sensoria are about half way down the toothed blade, not at the base as in Mexican *A. mombinpraeoptans*. The same

is true of an undescribed form resembling *A. serpentina*. In the example used, however, the complete arrangement of the peg sensoria does not occur. On one side one of the pegs is missing. On the other side the distal sensorium is missing. Such a situation is unusual. It may indicate that the series of examples appearing in one lot of material is an erratic series. It is not the intention here to discuss this form other than to show a method for its differentiation.

The ovipositor of *Anastrepha serpentina*, with the pegs in the center of the blade and about nine ventral sensoria on each side up to the proximal peg, is characteristic. This and the bright markings of yellow and deep brown make the species very conspicuous. The clasper of the male, figure 71, is also characteristic, since each clasper presents a definite shoulder. The larvae and the distinguishing features of the interspiracular processes have already been mentioned.

The male claspers of *Anastrepha ludens* are shown in figure 37, *B* (p. 74), and it will be seen that, while they are of the same general type as those of *A. serpentina*, they lack the shoulder, being simply triangular. Their shape and the characteristics figured distinguish

FIGURE 71.—Claspers of the male of *Anastrepha serpentina*, showing shoulders.

them from those of the other Mexican species, although some of these are rather like *A. ludens* in these points.

The ovipositor tip of *Anastrepha ludens* is shown in figure 37, *C*, and it will be seen that the blade of the ovipositor differs distinctly from that of *A. serpentina* (fig. 70, *B*) in its dentition, in the location of the peg sensoria nearer the base, and in the much smaller number of ventral sensoria. There are usually three pairs, and sometimes a closer fourth pair as shown distad of the first of the pit pegs.

A spiracular plate of the larva of *Anastrepha ludens* is shown in figure 14, *A*. The points in which it differs from that of *A. serpentina* (fig. 61, *A*) are at once apparent. The processes have a characteristic appearance, more bristlelike than those of most other species.

Up to the present time the possible importance of *Anastrepha serpentina* to the United States is not clear, but from the Mexican viewpoint it is important, because it heavily infests the sapote and related fruits. The infestation is so high in tree-ripe fruits that in parts of the country where these fruits are grown, especially in Veracruz, the growers do not permit them to mature on the trees, but pick them green and artificially ripen them to avoid infestation. Fruits that are so handled are far inferior in quality, in the authors' opinion, to those

that are allowed to mature normally. In spite of this practice, infestation still takes place to some extent, and, because of the attacks of the species, markets that would otherwise be open to these tropical fruits are closed.

From the point of view of the United States there are other factors involved. In the earlier days *Anastrepha serpentina* was not recorded north of Mexico City excepting along the west coast. It was believed to be a tropical form confined to tropical fruits such as sapotes. In 1933, however, adults were reared by members of the Mexican Department of Agriculture from peach from Ramos Arizpe.[43] Work by members of Hoidale's staff in the Rio Grande Valley of Texas recorded larvae in apple,[44] pear,[45] peach,[46] and quince [47] originating in the same location. Stone [48] found in the laboratory in Mexico City that females would adopt grapefruit for oviposition and that the larvae would mature therein as readily as would those of *A. ludens*. Zetek,[49] working at the Canal Zone laboratory, discovered larvae appearing in market oranges in Panama City which, when reared, proved to be those of *A. serpentina*. And in 1939 larvae of *A. serpentina* were found in one instance infesting grapefruit in the Rio Grande Valley of Texas.[50] Recent work by Shaw in that part of the Republic extending from San Luis Potosí to Tampico is revealing infestation by *A. serpentina* in various wild and cultivated fruits, and the data on this work are being assembled.

All this newer knowledge may have a definite bearing on the large populations of *Anastrepha serpentina* which, trap records show, usually appear annually in the Rio Grande Valley of Texas. With the exception of the one record from grapefruit, however, no infestation by the species has been found in Texas and the appearance of such large adult populations there remains to be explained. These populations, like those of *A. ludens*, appear and then disappear. The situation back of these adult populations has not yet become clear, but work was begun on the species in conjunction with that on *A. ludens* to obtain as much information as possible. Preliminary toxicity studies indicated that *A. serpentina* is as susceptible, if not more so, to the same types of poisons that will destroy *A. ludens*. Therefore any insecticide treatment developed for *A. ludens* would probably be equally valid for *A. serpentina*. The capture of the adults in numbers in the sugar lures employed for *A. ludens* in the Rio Grande Valley demonstrated that the lures used in traps for *A. ludens* can be used also to obtain an index to the population fluctuations of *A. serpentina*.

Since little was known of the biology of *Anastrepha serpentina*, Stone began work with the species at the laboratory. First he submitted the following fruits under equal conditions to adults of both *A. ludens* and *A. serpentina:* Grapefruit, orange, sour orange, limón dulce, sweet lime, sour lime, and navel orange. Females of *A. serpentina* punctured grapefruit, sweet orange, navel orange, and sweet lime during the first 2 hours, whereas *A. ludens* punctured

[43] See manuscript report 45, p. 153.
[44] See manuscript report 81, p. 154.
[45] See manuscript report 83, p. 154.
[46] See manuscript reports 87 and 88, p. 155.
[47] See manuscript report 89, p. 155.
[48] See manuscript report 52, p. 153.
[49] See manuscript report 58, p. 154.
[50] See manuscript report 90, p. 155.

all fruits but the grapefruit, which it avoided. The grapefruit, however, was badly infected by mold. Earlier, Stone had shown that grapefruit serves as a suitable host for the larvae of *A. serpentina*, which develop in it with about the same facility as do larvae of *A. ludens*. The flies also infested Natal plum and pear, in which the larvae lived satisfactorily. Kumquat was infested at the same time, but owing to the molding of the fruit the larvae did not survive. California cherries were also infested,[51] and Stone found peach to be such an excellent host that in the absence of chicozapotes peach was used for the rearing of laboratory populations for miscellaneous studies.[52]

Stone[53] conducted a series of oviposition tests comparing oviposition resulting when the flies had daily access to fruit for laying and when they were given fruit only once a week—an effort to simulate conditions with abundant fruit in the field and its scarcity. A marked difference occurred as shown in figure 72, representing oviposition per week by 10 pairs in each series. The flies having a daily opportunity to lay not only laid many more eggs but reached their maximum oviposition in the third week, whereas those with rarer opportunities reached the peak in the fourth week. There appears to be no obvious explanation for the drop in both cases on the thirteenth week and the subsequent rise.

The results, however, appear to show that a heavier infestation would be expected with a large amount of fruit available than when fruit is scarce. It has often been assumed that where fruit is very scarce there would be a concentration of laying in it, but this idea is not supported by the data. This may account for the fact observed with *Anastrepha ludens* in Santa Engracia that occasional scattered grapefruit maturing after the crop had all fallen was more lightly infested than was the fruit when it was very thick upon the trees. On the other hand, this may have been a reflection of the other fact observed from the chart, that with abundant fruit much of the laying is done early in the life of the females.

Those females that laid the greatest number of eggs were tested to determine if viability appeared to decrease, but this was not the case. Eggs Nos. 546–551 of female No. 62 were incubated and all hatched. Eggs Nos. 648–654 and Nos. 676–682 were incubated and all hatched. It seems evident, therefore, that even when individual flies lay up to 600 eggs these remain fertile. It must be remembered, however, that these flies were laying over a period of only a month and a half and were not very old flies like those of *Anastrepha ludens* discussed on page 78, when some of the eggs were found not to be viable.

The figure carries the comparison to the end of the twenty-ninth week, and it will be seen that the flies that had continuous opportunity stopped laying after the first 21 weeks while the others continued to lay for 8 weeks longer. Another interesting point brought out by these experiments is that the length of life of those females that have the most continuous opportunity to lay is shorter than of those which do not.

Detailed biological studies on *Anastrepha serpentina* have, up to

[51] See manuscript report 67, p. 154.
[52] See manuscript report 50, p. 153.
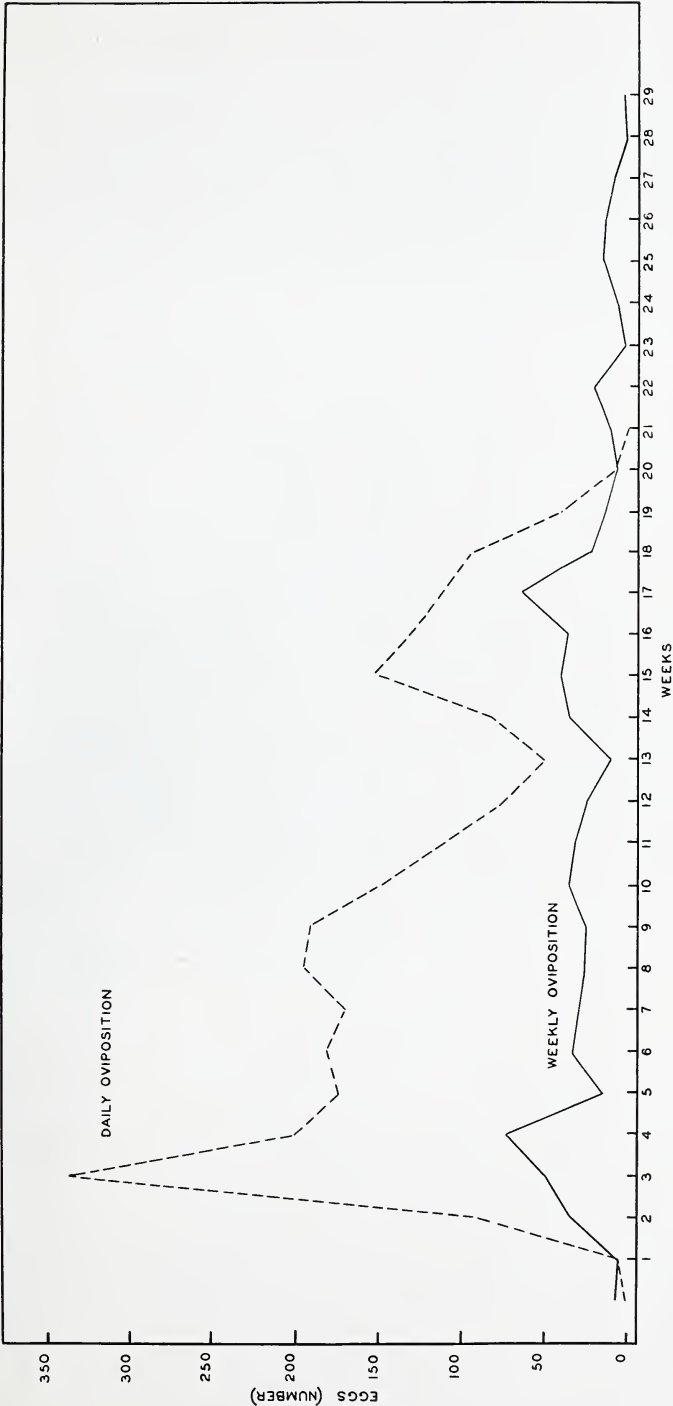[53] See manuscript report 66, p. 154.

FIGURE 72.—Oviposition of adults of *Anastrepha serpentina*.

the present, covered only the field of oviposition as here discussed. Stone has shown, however, that the adults may live more than a year. From an individual female, No. 65, he has recorded the deposition of 700 eggs.

In connection with his oviposition studies with *Anastrepha serpentina*, Stone [54] found a definite daily rhythm of egg laying. Under a constant temperature of 77° F. and constant artificial light, under this same constant temperature and normal daily change in light, and under fluctuating room temperature and normal daily light, the peak of egg production was at 4:30 p. m. Under constant darkness, however, and constant temperature, the peak was shifted to 10:30 p. m. A comparison is shown in figure 73.
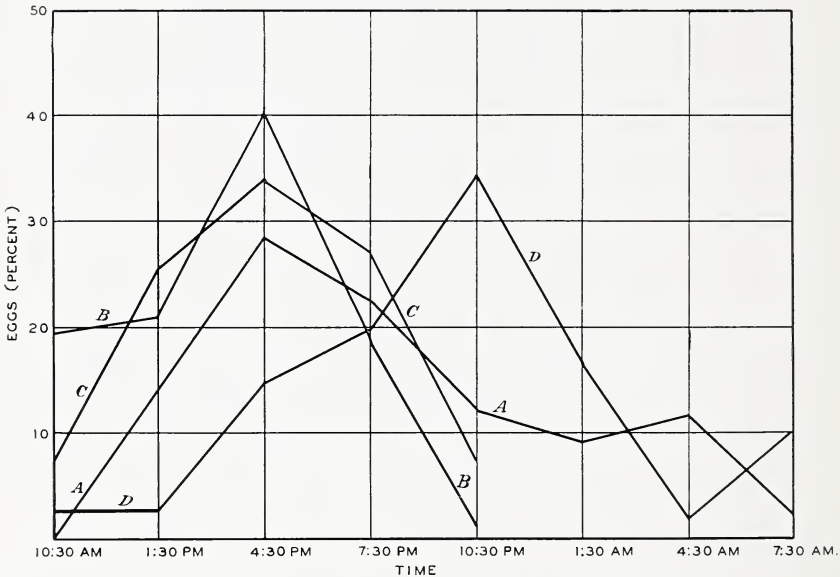
FIGURE 73.—Percentage of eggs of *Anastrepha serpentina* laid under the following conditions: *A*, At 77° F. and constant artificial light; *B*, at 77° and naturally fluctuating daylight; *C*, at room temperature and with fluctuating daylight; *D*, at 77° and in total darkness.

ANASTREPHA STRIATA Schin.

Anastrepha striata is seldom known to attack fruits other than the guava or those very closely related to it. The importance of the species therefore is entirely related to guava production. In Mexico, where guavas are everywhere grown and esteemed by the people generally, the fly is a factor of importance; but in the production of subtropical fruits, such as citrus, it is not involved.

Baker [55] reported that a fruit sold in the market of Tepic, Nayarit, under the name of "arrayan" is infested by *Anastrepha striata*.

In the early days of the work against *Anastrepha ludens* in Mexico, the larvae in guava and those in mango and orange were confused, and the high infestation in wild guavas led those in charge of the

[54] See manuscript report 63, p. 154.
[55] See manuscript report 56, p. 154.

campaign in Morelos in 1900–1901 to believe that they were making little headway, although very distinct reductions in grove infestation were being obtained.

Unless guava production is involved, *Anastrepha striata* may be largely ignored. It differs from the other commoner species in Mexico in that it is strongly attracted to decomposing protein lures, which may be used in traps if a population index of *A. striata* is desired.

Anastrepha striata is the species that so abundantly attacks guava throughout the central and southern parts of the Mexican Republic. It occurs in the northern regions, but there it is largely replaced by
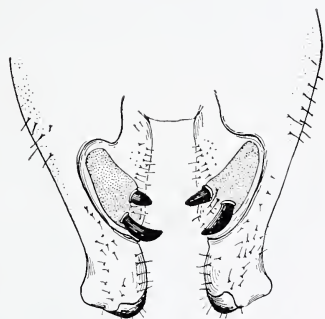
FIGURE 74.—Claspers of the adult male of *Anastrepha striata* showing teeth, etc.

FIGURE 75.—Tip of ovipositor of female of *Anastrepha striata* showing absence of marginal teeth.

a species of the *fraterculus* group which will be discussed under that name.

The claspers of *Anastrepha striata* (fig. 74) differ strikingly from those of either *A. serpentina* (fig. 71) or *A. ludens* (fig. 37, *B*) by being much larger and having the shoulder very near the tip, which is upturned. None of the three could well be confused. So also the ovipositor tip of *A. striata* (fig. 75) differs from that of the other two. It is quite without teeth. The point curves sharply outward to a broad base corresponding to the width of the ovipositor itself. The

lateral pegs are placed very near the tip before it begins to enlarge, and there are usually three ventral sensoria distad of these pit pegs and about five to the base of the proximal peg. The shape of the ovipositor, the lack of marginal teeth, and the location of the sensoria at once differentiate *A. striata*. The wing of *A. striata* is rather characteristic (pl. 7, *B*).

Between larvae of *Anastrepha ludens* and those of *A. striata* the difference is even more striking. Figure 76 represents the first spiracle of *A. striata*. The right-hand figure is from a slide made in January 1933 to show the spiracular processes. That on the left is from a larva selected at random from a population in guava in December 1937. The number of processes, the elongate base from which

1937.   1933.
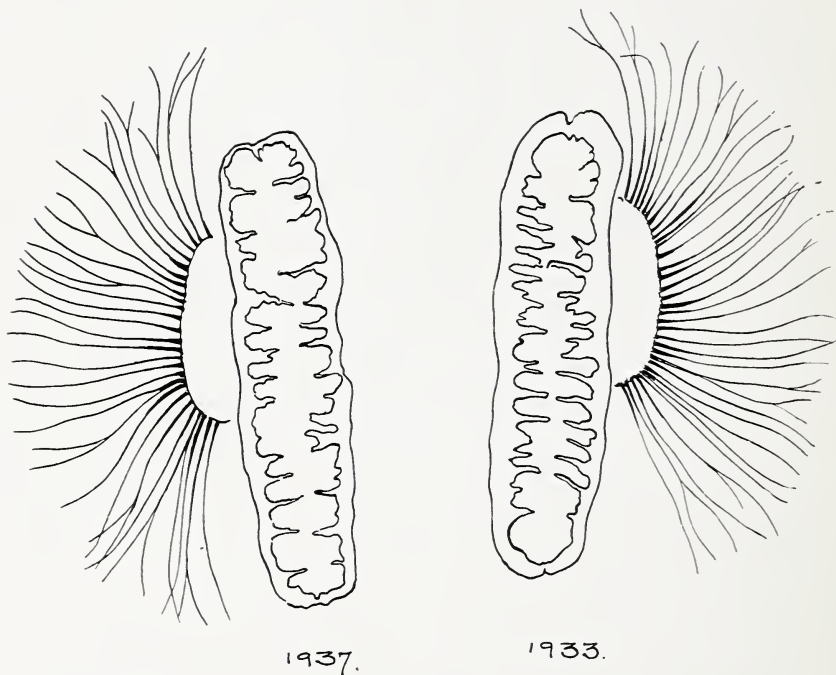
FIGURE 76.—First spiracle of larvae of *Anastrepha striata* taken in different years.

they arise, their fringelike appearance, and the location of the base in relation to the spiracle all differ strikingly from those of *A. ludens*.

ANASTREPHA DISTINCTA Greene

The Mexican material from *Spondias* was originally determined by specialists as *Anastrepha fraterculus*. The senior author, however, used the expression "Mexican *A. fraterculus*" to indicate that this Mexican form is not the species described as *A. fraterculus*. The *Spondias* feeder will be discussed in some detail later (p. 134). In trap material from Cuernavaca there occurred commonly a species which fulfilled the description of *A. fraterculus*, especially the character of the wing (pl. 7, *C*), and that name the senior author assigned to it at

the time. He [56] determined its biology by tying it up with the plant genus *Inga*, and rearings of the species were regularly made thereafter from *Inga* pods. *Inga* was found infested in the west as well as in the Morelos region.

This *Inga* feeder in Mexico is distinguished from the *Spondias* feeder by the longer ovipositor sheath of the female and by the character of the ovipositor itself (fig. 77). The peg sensoria are located very near the base of the toothed blade, and there are about 5 ventral sensoria on each side, distad of the location of the peg pits, with about 10 pairs in all. There are approximately 10 teeth on each side.

A very simple way to distinguish the *Inga* from the *Spondias* feeder is by the fact that the wing pattern of the form from *Spondias* is nearly always connected, whereas in the *Inga* feeder it is not. This
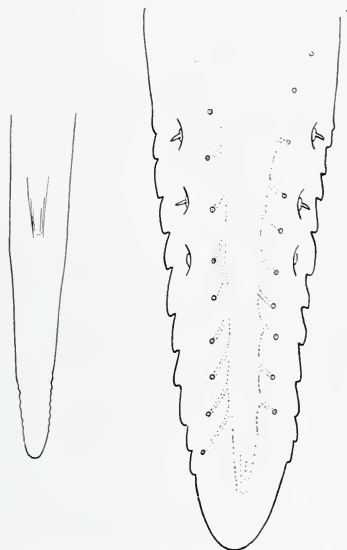
FIGURE 77.—Tip of ovipositor of *Anastrepha distincta* bred from *Inga*.

character is not absolutely dependable, however, and should males occur in which the wings appear alike it is difficult to separate the two superficially. In such case the claspers may be used, the ratio between length from tip to teeth and width at the teeth being different. In the *Inga* feeder this is about 5.9 as compared with about 4.6 in the *Spondias* feeder.

In 1934 Costa Lima (6) published on the genus *Anastrepha* and attached the name *A. fraterculus* to a *Spondias* feeder in Brazil, which, however, differs from the *Spondias* feeder in central Mexico. He described the Brazilian *Inga* form as a new species under the name of *A. silvai*. *Anastrepha silvai*, however, according to studies just completed by Alan Stone (41), proves to be a synonym of *A. distincta* Greene. The Mexican *Inga* form will therefore be discussed under the name *A. distincta*.

The importance of *A. distincta* in Mexico is largely dependent on

[56] See manuscript report 53, p. 153.

the fact that *Inga* pods are shipped throughout the country as an article of food and the seeds are used for growth in pots, under the name of "jinicuil." Infestation in them, therefore, is probably of some importance. The infestation is sometimes fairly high, but it is questionable whether it reaches a point of influencing the total production materially.

The *Inga* feeder in Panama differs slightly from that in Morelos, and it may be that a study of material from different regions will prove that there are several closely related forms attacking *Inga*.

W. E. Stone has studied the Mexican *Anastrepha distincta* in the laboratory from populations reared from *Inga* in order to determine whether the species would attack cultivated fruits as well as the pods in which it has been found. In this work he gave mated adults access to numerous fruits and other products. In most of these cases, however, *Inga* pods of suitable maturity were not available to the flies at the same time. The products offered *A. distincta* in the laboratory at different times, depending on the populations available, were as follows: Peach, sweet orange, lima grande, calabaza, banana, guava, avocado, chili pepper, sweet pepper, tangerine, *Physalis* sp., pear, grape, yellow sapote, and apple. Larvae resulted in lima grande, chili pepper, apple, and yellow sapote.[57]

ANASTREPHA MOMBINPRAEOPTANS Seín

One of the important species of fruitflies in Mexico feeds abundantly in *Spondias*, a fruit in common use, sold on all fruit stands. This species has had a series of names. It was for a time determined by specialists as *Anastrepha fraterculus* and under that name it has appeared in the earlier publications and reports of the Mexican laboratory. The senior author, however, to distinguish it from typical *A. fraterculus*, used the designation Mexican *A. fraterculus*. Later, in a review of the genus by Greene (*18*), the name *acidusa* Walk. was assigned to it. The laboratory then adopted the name Mexican *acidusa*, since the identity of *A. acidusa* itself was in some question. Recently Alan Stone (*41*) has pointed out, on the strength of examinations by Howard and Smart, that the type of *A. acidusa* is very different, and has determined the Mexican material as *A. mombinpraeoptans* Seín, a name given to the *Spondias* feeder in Puerto Rico. This established the proper name for the form in the West Indies, but, in the belief of the senior author, it does not entirely clear up the matter for Mexico, since differences are visible between *Anastrepha mombinpraeoptans* and the feeder in *Spondias* in Morelos with which the laboratory has worked.

Puerto Rican specimens selected at random show an angulation to the wing markings which differs from that shown generally by specimens from Morelos. This difference may be seen in the angle made by the two distal bands. *E* and *G* of plate 7 represent wings from Mexico, *E*, a wing from Cordoba, *G*, a wing from Morelos. Plate 7, *F*, represents a wing from Puerto Rico. The difference in angulation is at once apparent.

This difference may not be sufficient to separate individuals of West Indian populations invariably from those of central Mexican popula-

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[57] See manuscript report 55, p. 153.

tions, but it coincides with differences that have been noted in the host habits of the two forms. In Puerto Rico *Anastrepha mombinpraeoptans* is a decided pest of mangoes, one of the limiting factors in mango production there. In Morelos, however, the *Spondias* feeder rarely, if ever, attacks mango, even when *Spondias* and mango are growing together. Apparently also there are some differences in larvae taken at random in Morelos and in Puerto Rico. Figure 78, *A*, represents the first spiracle of a larva taken at random by L. C. Mc-
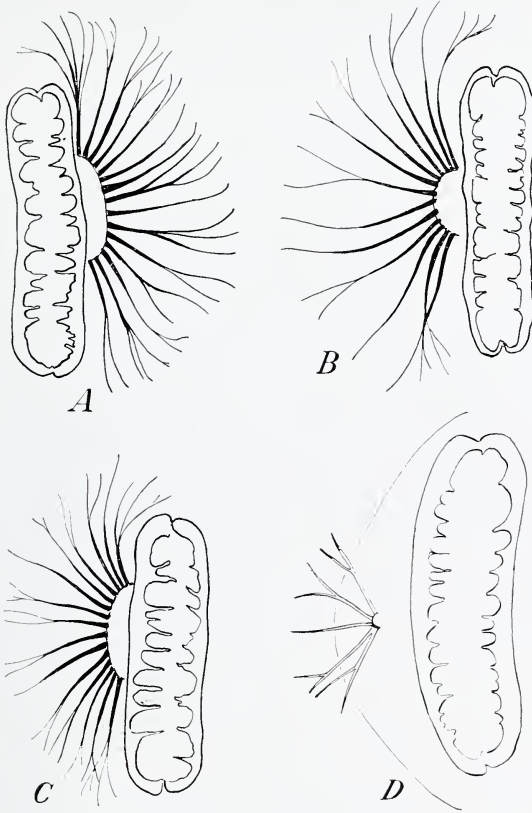
FIGURE. 78.—First spiracles of fruitfly larvae, showing interspiracular processes: *A, Anastrepha mombinpraeoptans* from Puerto Rico; *B,* Mexican *A. mombinpraeoptans; C,* Mexican *A. fraterculus* from tropical almond in Veracruz; *D, Toxotrypana* sp. from talayote.

Alister, Jr., in Puerto Rico and figure 78, *B*, represents the corresponding structure of a larva taken at random from *Spondias* in Morelos. It will be seen that the processes in the two cases are somewhat different, and the spiracle of the form from Morelos appears to be somewhat more slender. No long series of comparisons has as yet been made, but these noticeable differences as well as the differences in habits have led the senior author to adopt the designation Mexican *A. mombinpraeoptans* for the form with which the laboratory has worked. They indicate at least that the question of possible races

or species should be thoroughly investigated. In this connection the senior author has examined a larva from *Spondias* grown on the west coast. It showed a heavy fringe of spiracular processes arising from an elongate base. It is evident therefore that larvae with different characteristics may be found in *Spondias* in Mexico, and a knowledge of the situation must await a study of adequate material from different locations.

In the city of Veracruz Stone found tropical almond (*Terminalia catappa*) infested by a species closely resembling *Anastrepha mombinpraeoptans*. Figure 78, *C*, represents the first spiracle of a larva taken at random from this fruit. It will be noted that it resembles the corresponding structure of the larva of *A. mombinpraeoptans* from Puerto Rico. This emphasizes the importance of a detailed study of larvae from all hosts in all locations. The form from almond will be more fully discussed under the name *A. fraterculus*.

To illustrate the native habitat of the different fruitflies, an ellipse may be drawn to enclose the West Indies, to include the Florida Keys, and to touch the tip of Florida and that of Yucatán. These are separated from the mainland of Mexico by the expanse of the Gulf. It would be expected, therefore, that native fruitflies in the West Indies would be found on the Florida Keys and possibly on a fringe of the tip of Florida and Yucatán. Those in interior Mexico, lower Texas, etc., however, would be expected to be different. As a matter of fact, there appear to be these two distinct fruitfly faunas, and the realization of that fact is of considerable advantage in an understanding of why *Anastrepha ludens* and other forms are absent from the West Indies, and why forms on the Florida Keys are like those in the West Indies. In neither region should the flies be looked upon as importations there, but as native insects with the usual fluctuating cycles of abundance.

The eggs of the common species were studied by Emmart [58] (*15*), who recorded means for their differentiation. Their differences in size, shape, and surface markings are shown in figure 79, *A* and *B*. The fact that the eggs of Mexican *Anastrepha mombinpraeoptans* are stalked had been known for a long time, and this stalked egg had previously been figured in manuscript by Zetek. But according to Emmart's study the egg is twisted as shown in her figure. This twisting appears to be unusual, but time has not been available in which to verify this character on eggs from different regions. The few eggs studied by the senior author have not shown this twist. The eggs studied, however, were laid on the surface of fruit and were not embedded in it.

The status of the mango infestation in certain parts of the State of Veracruz remains to be studied. The point of interest to be cleared up in that connection is whether the individuals attacking mango there are like the typical form that infests the mango crop in the West Indies or are like the form in Morelos that seldom attacks mango.

Mexican *Anastrepha mombinpraeoptans* has been reared by W. E. Stone in large numbers from *Spondias* and has been tested by him on a considerable variety of fruits and vegetables. Like *A. ludens* and *A. serpentina*, it has been given access to host material at different times and under different conditions. Stone tested it on apple, avocado,

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[58] See manuscript report 27, p. 153.

banana, calabaza, akee (*Blighia sapida* Koenig), chili pepper, fig, grapefruit, grapes (white and purple), sweet lime, pomegranate, lima grande, mango, mombin (yellow), *Opuntia* sp., orange, peach, pear, perón (apple), *Physalis* sp., yellow plum (*Prunus* sp.), quince, and tangerine, but the only fruits infested were fig, yellow mombin (*Spondias* sp.), and the yellow plum (*Prunus* sp.).

The mombin is the natural host of this Mexican form, and heavy infestation of it was looked for. The plum, however, served so well as a host that Stone used it for rearing populations when *Spondias* was not available. He was never able to get mangoes infested although they were, at the same time, abundantly infested by *Anastrepha ludens*
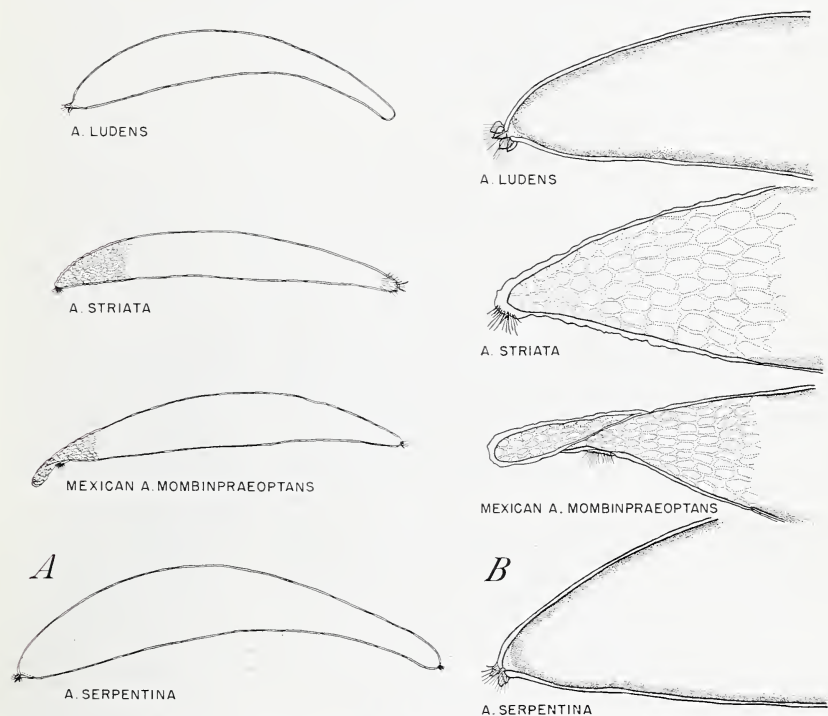
FIGURE 79.—*A*, Eggs of *Anastrepha ludens, A. striata*, Mexican *A. mombinpraeoptans*, and *A. serpentina; B*, details of the micropyles of the eggs. All highly magnified. (After Emmart (*15*).)

in adjoining cages. If this form is identical with the mango pest of the West Indies, it seems unusual that it would refuse mangoes. Under artificial conditions it did refuse them, as it apparently does in the field. At a later date Stone [59] obtained infestation in green peaches after unsuccessful experiments with ripe peaches. The population used, however, had been reared from rose apples from Cordoba. This led the senior author to make a study of the adults remaining in the cages, and a few specimens of the species here considered under the name *fraterculus* were discovered. The probability is, therefore, that these were responsible for the infestation in peach.

[59] See manuscript report 59, p. 154.

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In duration of life Mexican *Anastrepha mombinpraeoptans* almost equals that of *A. ludens* or other species. Stone has maintained individuals in the laboratory for many months. One individual lived 1 year and 44 days.

Apparently temperature factors are of importance in limiting the distribution of this species. In Cuernavaca, where *Anastrepha ludens* is abundant, Mexican *A. mombinpraeoptans* is much less abundant than it is in municipalities only a short distance away that are lower and warmer. Stone [60] made a count in October of the number of larvae of this species occurring in *Spondias* fruits from three locations in Morelos on the same road and relatively near together, but of different altitudes. His figures are given in table 8.

TABLE 8.—*Occurrence of larvae of Mexican Anastrepha mombinpraeoptans in Spondias in Morelos, 1934*

Locality	Fruit	Larvae	Approximate altitude
	Number	*Number*	*Feet*
Yautepec	1,590	2,386	3,750
Xiutepec	1,810	1,849	4,250
Cuernavaca	1,493	35	4,750

ANASTREPHA FRATERCULUS Wied.

The *Spondias* feeder in central Mexico has been confused with other forms superficially like it. One of these attacks peach in the more northern parts of the Republic. There has been no opportunity as yet to study this deciduous fruit situation, the importance of the species attacking peach, or the response of that species to environmental conditions.

The form attacking peach agrees with a species abundant in guava in the north, which there replaces *Anastrepha striata*, the dominant form in guava in central and southern Mexico. This guava species the senior author segregated as undescribed, and it has been carried under his manuscript name in the manuscript reports from the Mexican laboratory. Although it is the dominant form in guava in the north it is seldom reared from that fruit in Morelos. In Cuernavaca Plummer reared approximately 10,000 adults of *A. striata* from guavas and during the same period was able to obtain only 16 specimens that he could assign to "*A. fraterculus*." Since this species attacks peach not uncommonly and since it is trapped in large numbers in the Rio Grande Valley of Texas its identity becomes of considerable importance.

Anastrepha fraterculus (Wied.) is a South American species. It attacks various fruits including peach, *Citrus*, guava, *Spondias*, and *Eugenia*. Alan Stone (*41*) believes it to be a very variable species ranging from Texas to central South America. He identifies the Mexican material from peach and guava as *A. fraterculus*. The senior author prefers, however, to consider the Mexican form distinct from *A. fraterculus*. Since differences between the two forms exist, it seems wisest to consider them different unless biological studies both in

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[60] See manuscript report 52, p. 153.

Mexico and in South America supply data to prove them identical. Such data do not exist. To avoid using a new name, however, the Mexican species is distinguished in this publication as Mexican *A. fraterculus*. The laboratory staff has reared this Mexican species from peach, guava, and rose apple, and what appears to be the same thing from tropical almond, a fruit not recorded as a host of *A. fraterculus*.

Anastrepha fraterculus possesses wing markings that differ from those of the Mexican form. The inverted **V** is separated from the main pattern, the wing thus resembling that of *A. distincta*. The Mexican form has the inverted **V** connected with the main pattern, the wing thus resembling that of *A. mombinpraeoptans*. This difference is shown in plate 8, which depicts a wing of *A. fraterculus* from sour orange from Brazil (pl. 8, *A*) and wings of Mexican adults reared from peach (pl. 8, *B*), guava (pl. 8, *C*), rose apple (pl. 8, *D*), and tropical almond (pl. 8, *E*). Only a limited number of Brazilian specimens are available to the senior author. These all show the typical markings of *A. fraterculus*. According to descriptions, occasional specimens occur in South America in which the inverted **V** is connected, and some specimens can be found in Mexico in which the connection fades out. But populations as a whole may be separated by this character. When the connection is broken in Mexican specimens, as in plate 8, *F*, these are usually males. This specimen was from rose apple from Cordoba. The pattern of the opposite wing, however, retained a connection. The ovipositors, too, seem to differ slightly. Those of the Mexican specimens from all hosts appear more tapered at the tip than does that of *A. fraterculus* and the opening seems slightly farther from the distal extremity. These differences may be seen in plate 9 where the tip of an ovipositor of *A. fraterculus* from sour orange from Brazil (pl. 9, *A*) is shown in comparison with ovipositor tips of Mexican specimens reared from peach (pl. 9, *B*), guava (pl. 9, *C*), rose apple (pl. 9, *D*), and tropical almond (pl. 9, *E*).

No biological studies have as yet been made with material from peach and guava in the north. It may be, therefore, that when these have been completed they will show differences in responses between the northern populations attacking peach and guava and those in Veracruz attacking rose apples and tropical almonds. One point of interest is that, although populations in the north occur commonly in the vicinity of *Citrus*, no infestation in sour orange or other *Citrus* has been located by personnel from the laboratory.

Studies by E. W. Baker on Mexican *Anastrepha mombinpraeoptans* have yielded information on the form in rose apple. Infestation in rose apple is known to the laboratory only in the vicinity of Cordoba, Veracruz. E. W. Baker brought to the laboratory from Cordoba large numbers of infested rose apples in order to build up a stock of *A. mombinpraeoptans* from them. Experiments were begun on the duration of the egg stage in relation to temperature, flies from this stock being used. The accumulated data when plotted gave two distinct lines depicting response.[61] Two egg forms were noticed and from these the two lines were obtained. Adults from the stock cages were therefore submitted to the senior author, and preparations showed, besides Mexican *A. mombinpraeoptans*, specimens apparently agreeing with the guava form in the north. Data on the duration of its egg

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[61] See manuscript report 92, p. 155.

stage as influenced by temperature, when plotted with the reciprocal of time against temperature, gave a line definitely above that for *A. mombinpraeoptans*, although the two were parallel. Such lines for the Mexican species of *Anastrepha* so far studied fall one above the other reading from the lowest as follows: *A. ludens, A. serpentina, A. mombinpraeoptans*, and this species from rose apple. Until lines have been established from populations living in peach and guava in the north no attempt will be made to interpret these findings.

The form living in tropical almond has been noted only in the city of Veracruz. No biological studies on this form have been made with the exception of some observations by Stone. He reared populations from almond from Veracruz and gave mated adults access to *Spondias* from Morelos. The flies from almond did not lay in the *Spondias*. E. W. Baker, on the contrary, found that the flies from rose apple oviposited readily in *Spondias*. Tropical almond is not listed as a host of *Anastrepha fraterculus* in South America, but *Spondias* is one of the common hosts of that species. It would appear desirable therefore to conduct more detailed studies of the form attacking tropical almond before definitely assigning its position.
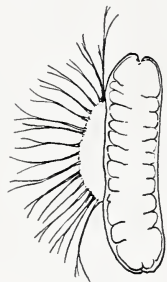

FIGURE 80.—First spiracle of larva of Mexican *Anastrepha fraterculus* from peach.

The larva of the form attacking almond possesses spiracular processes (fig. 78, *C*) that resemble those of the larva of *Anastrepha mombinpraeoptans* from Puerto Rico. The form from peach from the northern part of the Republic is very similar although the processes may form a fringe somewhat less dense in character. The spiracle of a larva from peach from Nuevo León is shown in figure 80. This figure and those of the wings and ovipositors given in plates 8 and 9 will serve to identify this Mexican species until further studies have been made.

ANASTREPHA CHICLAYAE Greene

A species of *Anastrepha* entirely yellow in body color, has been found for some years in the laboratory material. The wing (pl. 10, *A*) of this species is broadly rounded at the tip, which gives it a shortened appearance. The senior author has carried this species as new under a manuscript name. It is common about Santa Engracia and is frequently trapped in the Rio Grande Valley of Texas, but in Morelos it appears to be rare. In view of the fact that it occurs so commonly in Texas it is discussed in this publication in order to eliminate it from consideration of the economic problems there.
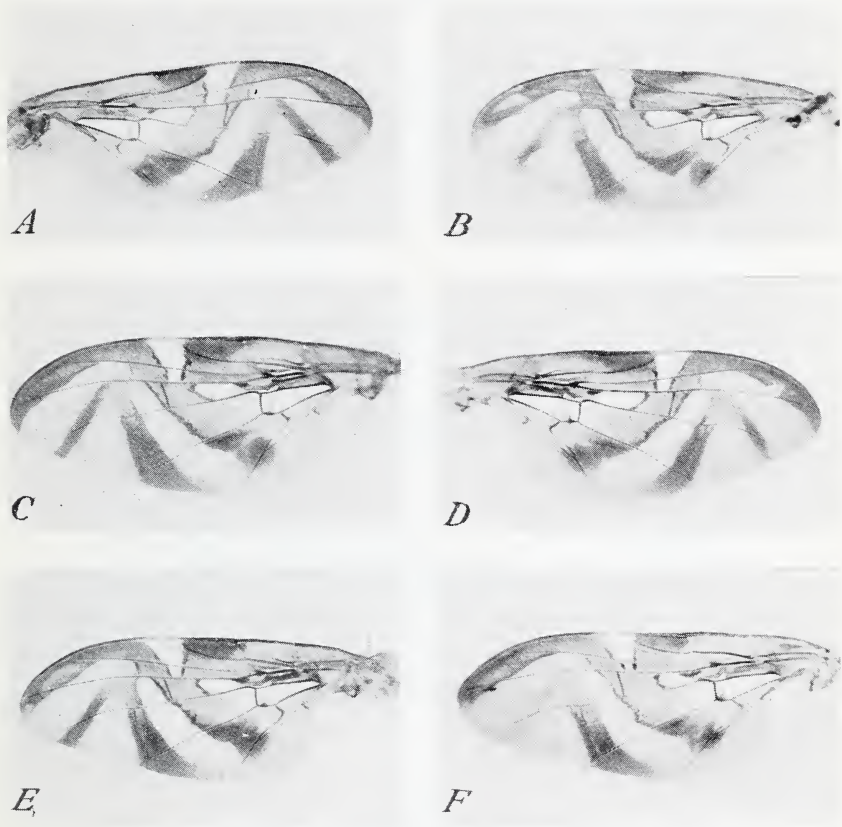
WINGS OF ANASTREPHA FRATERCULUS

A, Typical form from sour orange from Brazil; B, Mexican form from peach; C, Mexican form from guava; D, Mexican form from rose apple; E, Mexican form from tropical almond; F, Mexican form from rose apple showing broken pattern.
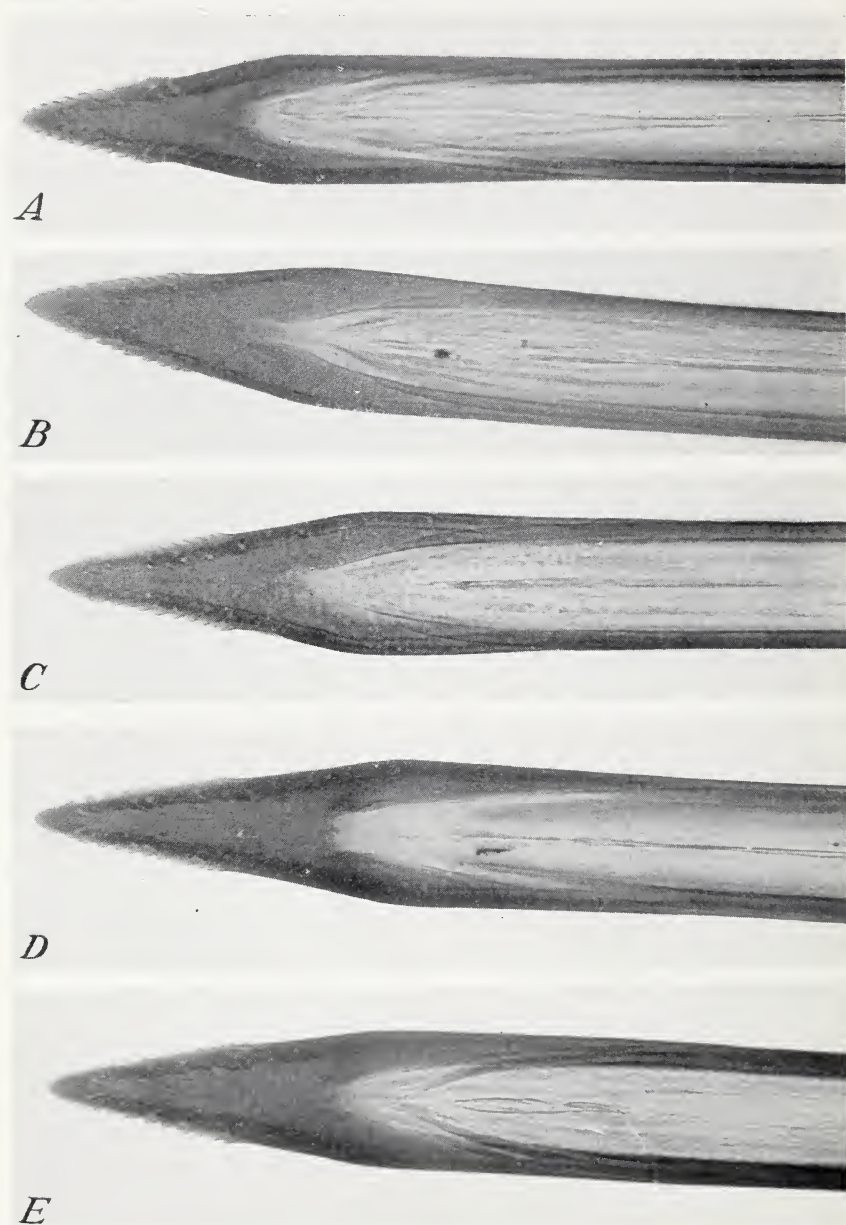
OVIPOSITORS OF ANASTREPHA FRATERCULUS

A, Typical form from sour orange from Brazil; B, Mexican form from peach;
C, Mexican form from guava; D, Mexican form from rose apple; E, Mexican form
from tropical almond.

WINGS AND OVIPOSITORS OF FRUITFLIES

A, Wing of *Anastrepha chiclayae;* B, ovipositor of *A. chiclayae;* C, ovipositor of Mexican *A. aphelocentema;* D, wing of Mexican *A. aphelocentema.*
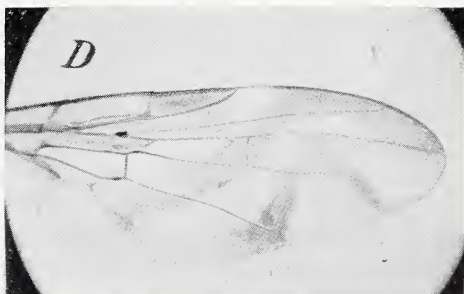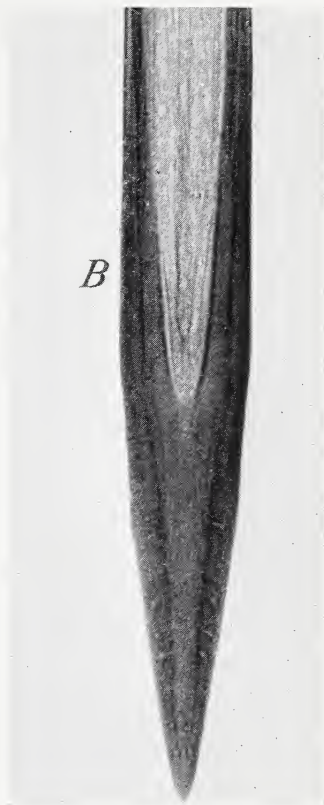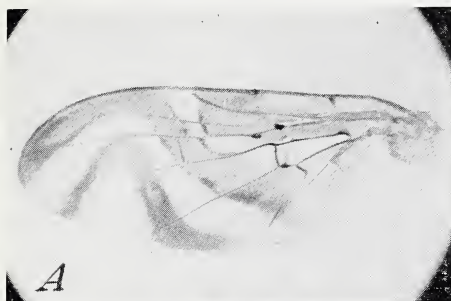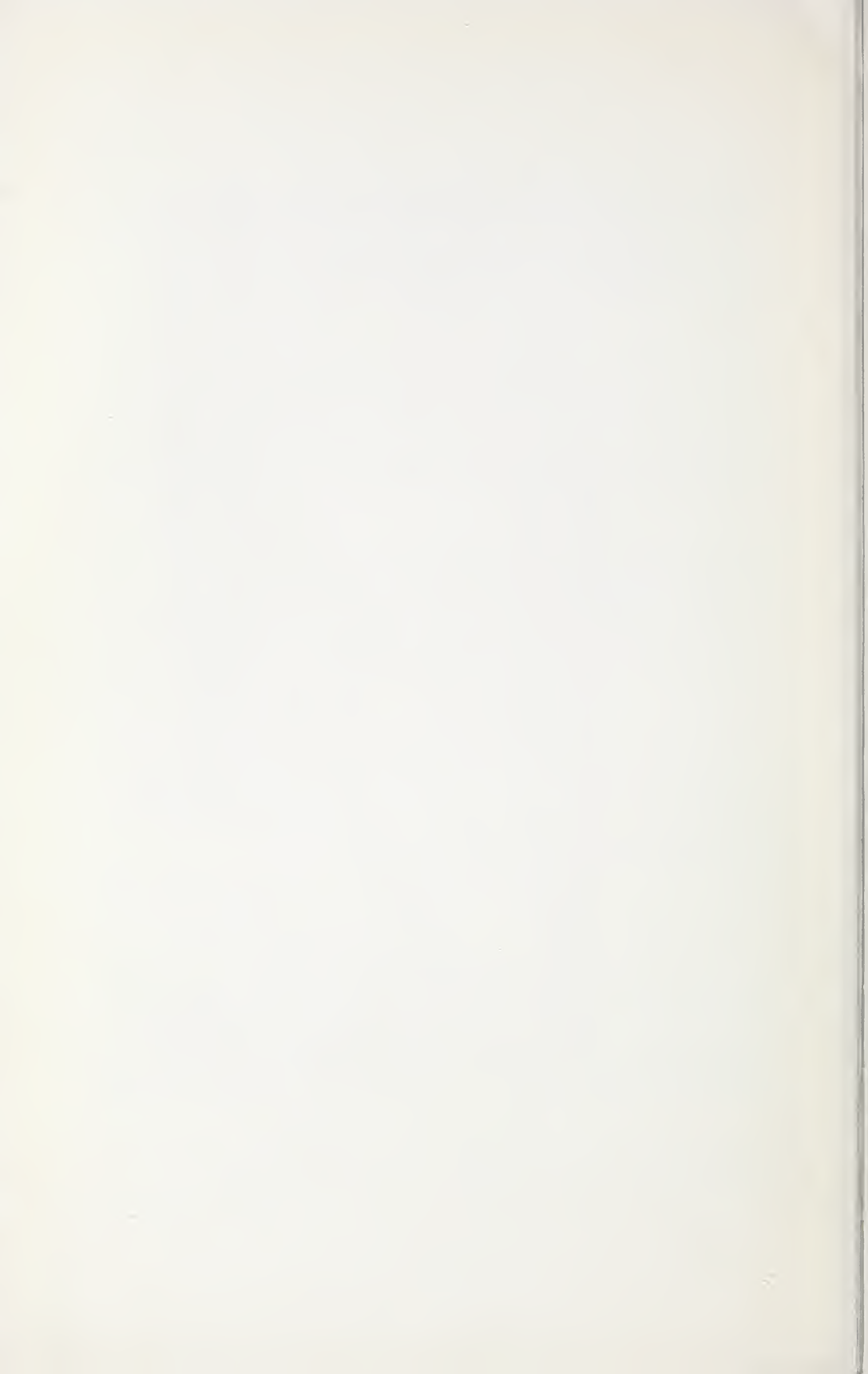
Alan Stone (*41*) identifies this species as *Anastrepha chiclayae* Greene, a form described from Peru. Greene's name, therefore, is adopted in this publication although the Mexican material differs somewhat from the form from Peru and it might, for this reason, appear wisest to retain the two as distinct. The species infests the amapola (maypop), a fruit belonging to the genus *Passiflora*. There is a group of species of *Anastrepha* all of which have a yellow or golden-yellow body color and all of which are associated with the plant genus *Passiflora*. This group includes *A. ethalia* Walker, *A. lutzi* Costa Lima, *A. limae* Stone, Mexican *A. chiclayae*, and probably others. It is a small, compact group that deserves further study with a view toward determining the range of the species in it and the biological and morphological limits of its forms. Since Mexican *A. chiclayae* is not known to attack fruits of economic importance, no studies have been undertaken with it. In fact it is only very recently that its wild hosts have been proved.

In October 1939 larvae were found in red and yellow amapola in the vicinity of Tampico Alto, Veracruz, by Shaw and R. E. Lecroy, and adults were reared from these larvae by Shaw. In May 1940 Plummer collected larvae in maypops at Tamazunchale, San Luis Potosí, and reared adults from them. Thus the hosts of this species, which appears commonly in the north of the Republic and in Texas, were established, and the populations that appear in the Rio Grande Valley may be disregarded insofar as *Citrus* and similar economic fruits are concerned. They represent moving populations similar to those of *Pseudodacus pallens*, the individuals of which may be captured in citrus trees although they have reproduced elsewhere.

The ovipositor (pl. 10, *B*) of this species tapers rather acutely at its tip, and the marginal teeth are very fine. The sensoria are delicate. The two distal of the three pairs of large pit-peg sensoria are located about midway along the serrated portion of the tip. They are perhaps slightly more distad in Tampico material than in material from Tamazunchale and Texas. The nature of the ovipositor and of the wing, both of which are shown in plate 10, will serve to distinguish *Anastrepha chiclayae* from the species attacking economic fruits.

ANASTREPHA APHELOCENTEMA Stone

On May 27, 1938, Monk [62] collected fruit of the socavite at Tamazunchale, San Luis Potosí, infested by larvae of an *Anastrepha*. The exact identity of this fruit is not yet known but it appears to be close to the species described by Pittier as *Lucuma standleyana*. The same fruit is widely attacked by *Anastrepha serpentina*.

Adults reared from these larvae proved to be superficially much like *Anastrepha ludens*. It is not improbable therefore that any material of this form that may have been collected in the early days was determined as *A. ludens*. *A. aphelocentema*, however, differs from *A. ludens* very distinctly in the structure of the ovipositor (pl. 10, *C*), which is without marginal teeth. For this reason the senior author assigned to it the name *Anastrepha aphelocentema*, under which name it has been described by Alan Stone (*41*). This lack of marginal teeth and the length of the ovipositor at once separate it from

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[62] See manuscript report 86, p. 155.

all other Mexican species, since the only other Mexican form possessing an ovipositor devoid of teeth is *A. striata*, and the ovipositor of that species is short. *A. aphelocentema* has been taken by Shaw a number of times since its original discovery, but always in the same host and in the same location. E. W. Baker, using a population from puparia obtained by Shaw, made oviposition tests with orange, grapefruit, sour orange, mandarin, kumquat, two varieties of lima, black sapote, yellow sapote, zapote mamey, peach, papaya, banana, apple, avocado, coffee berry, tejocote (*Crataegus* sp.), *Spondias*, tomato, pepper, citron, *Vincetoxicum*, and *Acacia* (?) sp.[63] In view of the fact that no larvae were reared experimentally in any of these fruits, the possibility of *A. aphelocentema* adopting citrus and related fruits of economic importance seems much reduced. The appearance of the wing (pl. 10, *D*) and of the ovipositor tip (pl. 10, *C*) of the species will permit the easy separation of *Anastrepha aphelocentema* from *A. ludens*.

Toxotrypana curvicauda Gerst.

The most common pest of papayas in Mexico is the papaya fruitfly, *Toxotrypana curvicauda*. This species occurs commonly in Florida, where it attacks the papaya. It has been reared in the laboratory in Mexico City in considerable numbers from papaya from Cuernavaca.

In the trapping work in the Rio Grande Valley and through the wild land of northeastern Mexico a fruitfly determined as *Toxotrypana curvicauda* has been commonly taken. Yet papayas growing in Texas have not been found infested, and only two cases of infestation in the Santa Engracia region have so far been noted. This peculiar situation led the senior author to study trapped material in comparison with that reared from papaya in Morelos. Distinct differences between the two were apparent. The flies of the papaya material are usually uniform in coloring, and the wings are generally angular. Those of the trapped material from the northeast of the Republic are smaller, brightly banded with yellow and black, and the wings are not generally angular but of a shape more resembling those of species of *Anastrepha*.

At Hacienda Santa Engracia McPhail[64] undertook to determine the source of this wild material of "*curvicauda*" and was successful in determining the insect's biology. The species is abundant in the fruit of a wild vine known as talayotillo or talayote, a plant belonging to the milkweed family. There are many similar fruits in this family all called talayote, and a differentiation of them has not yet been completed. The discovery of this as the host, however, as well as the noticeable differences between this brightly marked form and the flies from papaya, raises the question as to whether they are the same species. The talayote form is therefore maintained as distinct. The differences in the shape of the wings are striking, and the differences in the armature of the costal margins in the males may be seen in figure 81. *Toxotrypana curvicauda* possesses heavy spatulate spines on the margin, whereas those of the new form are more elongate and narrow.

[63] See manuscript report 91, p. 155.
[64] See manuscript report 66, p. 154.

Unfortunately, when McPhail was doing his biological work he assumed the species to be *Toxotrypana curvicauda*, since determinations had been so made; and while abundant adult material was reared, no larvae were preserved. In a subsequent season the form proved to
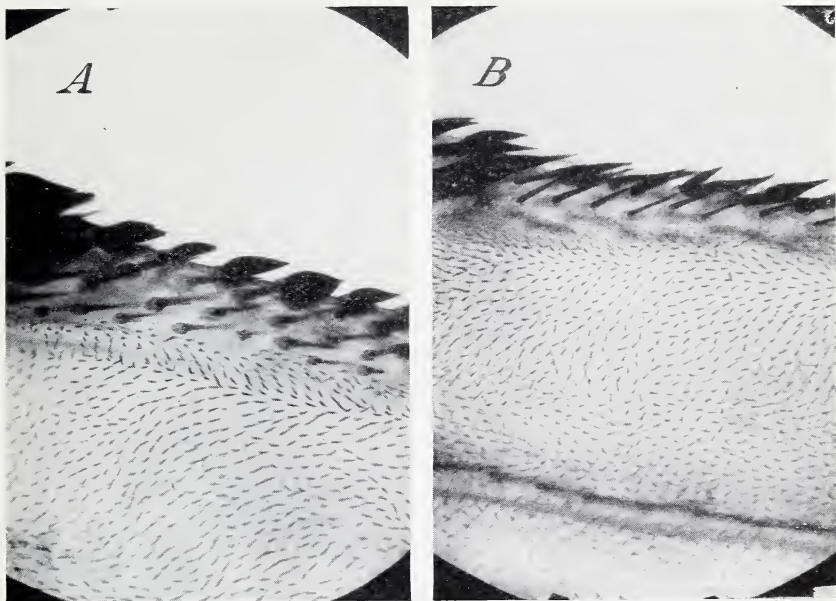
FIGURE 81.—Costal margins of wings of males of *Toxotrypana: A, T. curvicauda; B*, form from talayote.

be rare, but Plummer and Monk [65] obtained larvae from talayote near Cañon de Rosario close to Santa Engracia in February 1938. These larvae are large and suggest those of *T. curvicauda*, and it is probable that they are larvae of the new *Toxotrypana*. The first spiracle with its spiracular processes is shown in figure 78, *D*, for comparison with
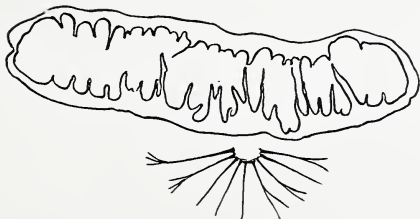
FIGURE 82.—First spiracle of larva of *Toxotrypana curvicauda,* showing processes.

that of *T. curvicauda* (fig. 82). The differentiation of these insects raises the economic question as to how far the new form attacks cultivated papaya, a question which has not yet been answered by biological studies.

[66] See manuscript report 85, p. 155.

STUDIES OF FRUITFLY DIFFERENCES AS RELATED TO DIFFERENCES IN HOST HABITS

As has been discussed previously, certain forms with different host habits appeared very similar morphologically and were frequently determined as identical. This led to the thought that populations exhibiting differences in host habits might show differences in the character of the chromosomes, and a cytological study was therefore planned.

This study was undertaken by Emmart (*16*). Unfortunately, she did her preliminary work on *Anastrepha ludens* rather than on the *Spondias* feeder and left Mexico before the study was well under way. Her first contribution, therefore, confined to *A. ludens* and to the spermatogonial and meiotic figures during spermatogenesis, gives the first description of the chromosomes of a species of *Anastrepha* but leaves untouched the problem of host races.

The difficulty in determining specimens when they are fragmentary and the necessity of developing different systems for larvae, puparia, and adults led to the hope that a method might be perfected which would be serviceable for all stages alike and for fragments as well as for entire specimens.

With Mooser's kind cooperation a serological study was undertaken with him at his laboratory by Baker in August 1932. One hundred freshly emerged, unfed flies were used in each instance. After decapitation and removal of wings, antisera were prepared from rabbits and tested against the different stages of the same species and against others. The study was continued later when other species began to emerge in numbers. While differentiation was obtained with parts of larvae, etc., the dilutions were not sufficiently wide to permit the method to serve as a practical one.

SUMMARY

The Mexican fruitfly (*Anastrepha ludens* (Loew)) is widely distributed in Mexico, where it attacks mango, citrus, and other fruits. The characteristic damage caused by the larvae is described.

The native home of the species is the northeastern section of Mexico, where it infests fruit of the yellow chapote (*Sargentia greggii*), an indigenous tree. Studies have confirmed field infestation of the following fruits: Cherimoya (*Annona cherimola*), custard apple (*A. reticulata*), white sapote (*Casimiroa edulis*), sour orange, grapefruit and shaddock, kid-glove oranges of the mandarin and satsuma types, sweet oranges, varieties of sweet limes, rose apple (*Eugenia jambos*), jinicuil (*Inga jinicuil*), mammee apple (*Mammea americana*), mango, peach, guava, pomegranate, pear, apple, quince, and the yellow chapote.

Fruits and vegetables infested under laboratory conditions include the following: Sapodilla (*Achras zapota*), cactus fruit of several varieties, fig, banana, English walnut, bell and chili peppers, tomato, squash, fruits of *Spondias* sp., loquat, papaya, *Cyphomandra betacea*, California cherry, cattley guava, Natal plum, Spanish plum, *Feijoa sellowiana*, pancolote, and tempixtle (*Bumelia laetevirens*).

Fruits unsatisfactory as hosts or not infested in the laboratory in-

clude lemons and sour limes, snap beans, lima beans, coma, (*Bumelia spiniflora*), cantaloup and honeydew melons, chayote, okra, cucumber, and chilacayote.

Grapefruit is evidently preferred for oviposition over orange, but heavy infestations may be a reflection of factors other than fruit preference. Mango is decidedly preferred over guava, and the selection of green fruit over ripe fruit is shown. As many as 117 larvae have been found in a single mango in Cuernavaca.

Selection of fruit by adults for feeding is less specific than the choice of fruit for oviposition, and for feeding the flies much preferred mango, either whole or cut, to orange, guava, or sugar solution. Fruitflies were observed feeding on the leaves of corn in Oaxaca and were frequently observed feeding on fallen mangoes. Flies restricted to water and a single carbohydrate lived for many months when given dextrose, levulose, galactose, maltose, sucrose, melezitose, raffinose, or dextrin.

The planting of grapefruit or sour orange trees to protect a sweet orange crop from infestation is not recommended. Old shaded citrus groves offer an environment very suitable to the fly, although fruit on small trees growing in open areas does not escape infestation.

In Cuernavaca mangoes offer almost continuous availability, and sweet lime, a minor host there, and off-season mangoes serve to maintain the fly population throughout the year. After the fruit has fallen from mango trees in Cuernavaca there are definite migrations of fruitflies to guava bushes in fruit, although the females seldom utilize guavas for oviposition. In Tequila the population of flies in citrus groves is high by reason of the earlier infestation in mangoes. In Tampico the sequence of citrus maturing throughout the year evidently maintains the fly population. Recent studies in Santa Engracia indicate that fly populations entering citrus groves in the fall were apparently produced in *Sargentia* in the summer. In Santa Engracia flies leave the groves in the spring even while fruit remains. Migration of flies to and from groves in Texas is discussed.

All data indicate that it is impossible to eliminate the fruitfly during the off-season summer months, since populations are widely dispersed throughout its native habitat. The maintenance of a host-free period in Texas during the summer, however, is of value in preventing the increase of the fly in other fruits shortly before early varieties of citrus mature.

The incubation period of the egg ranged from 5.5 to 9.5 days and from 6 to 12 days in studies carried on under natural variation of temperature in Cuernavaca. The larval period ranged from 18.5 to 35 days at a mean temperature of 70.52° F. The length of life varies in different fruits and was found to range from 15 days in figs to 32 days in mandarins under a constant temperature of 77°. There appears to be no uniform relationship between the length of the larval period and the pH value of the host fruit. In peppers the shortest larval periods were 54.25 days at 59°, 25.5 days at 68°, 16.5 days at 77°, and 14 days at 86°.

A detailed description of the larva serves to distinguish it from those of related species. Spiracular processes proved to be especially valuable as a means of differentiation.

Fruit containing 70,707 *Anastrepha ludens* larvae was sterilized by

the vapor-heat process at 110° F. and the larval mortality proved that an 8-hour approach followed by a 6-hour exposure at 110° F. with saturated vapor throughout the full 14 hours was sufficient to guarantee no survival. Results with the sterilization of mangoes were promising, those with citrus suffered from the character of the samples sterilized. Larvae of *Anastrepha striata* proved to be more resistant to treatment by this method than those of *A. ludens*.

In treatment of fruit by exposure to low temperatures, a security value of 99.997 percent mortality was indicated when fruit was held at 30° to 31° F. for 15 days, at 32° to 33° for 18+ days, at 33° to 34° for 20 days, or at 34° to 35° for 22+ days.

Several factors cause larvae to leave fruit. These include (1) gradually decreasing temperature, (2) rain or water falling upon the fruit, (3) shaking or jarring of the fruit, and (4) contact with moist rather than dry soil.

Various methods for the disposal of infested fruit are discussed. If fruit is buried under 18 inches of carefully packed soil, adult flies cannot escape.

Opius crawfordi is the most common parasite attacking larvae of *Anastrepha ludens*, but the percentage of parasitization is relatively low. Other species of parasites are of less importance. Predators such as the staphylinid beetle *Xenopygus analis* destroy fruitfly larvae in some numbers.

Puparia are usually formed in the soil, which the larvae enter upon leaving infested fruit. The length of time spent by the insect within the puparium is largely a function of temperature and ranges from 12 days at 87.8° F. to 107 days at 53.4°. Emergency of adults from moist soil was 69.3 percent as compared with 4.6 percent from dry soil. Some emergence of flies occurred from puparia of *Anastrepha striata* that had floated on water for 4 days. Exposure of puparia to 103.1° for more than 20 hours and at 104.9° for about 13 hours was required for a 100-percent kill. Pupae within newly formed puparia were more resistant to the effects of low temperature than those in 2-day-old puparia. Marked resistance was shown when the age reached 4 days.

A description of the adult *Anastrepha ludens* shows wherein it is distinguished from related species. Ovipositors of two types were found when specimens of *A. ludens* from different localities were examined.

Over 95 percent of the adults emerge from the puparia between 6 and 10 a. m. Exposure to sunlight or increase in temperature apparently stimulates emergence. Males tend to emerge before females.

The length of the premating period is probably dependent on temperature and was shown to range from 8 to 34 days. Males seem to reach sexual maturity before females. Unmated females, however, commonly deposit eggs. The female usually begins laying after the first mating and may continue laying irregularly during much of her subsequent life. One female laid 401 eggs. Few eggs are laid by very old females, and only a low percentage of these are viable. Viable eggs were produced by females as old as 9 months. Eggs are deposited through a puncture in the skin of the fruit made by the ovipositor of the female.

Mortality of adults of *Anastrepha ludens* was remarkably low when

flies held under natural variations of temperature experienced 32° F. or below on 20 occasions over a period of 2 months. During 11 of the last 13 days of this experiment a minimum of approximately 23.8° was recorded in the cages. The flies became fairly active during the day when the average noon temperature reached 63.5°. Flies are often killed, however, by high temperatures, especially if exposed to the sun. They seek the shaded sides of leaves and fruit during midday. Rapid kill of adults was recorded at constant temperatures ranging from 103.28° to 109.58°.

Of a total of 495 miscellaneous materials tested in different types of traps for attractiveness to adults, 69 showed some attraction for *Anastrepha ludens*, but only essence of white wine and resinol spikenard were attractive to any marked extent. Decomposition products of protein material such as casein, proved to be highly attractive to *A. striata* but showed little attraction to *A. ludens*. Fermenting sugar solution is attractive to *A. ludens*, and extensive studies were made on intermediate products of fermentation and the effect of added materials. Yeast in sugarless media gave very good catches, and yeast in dilute alcohol and yeast in water alone were promising. A seasonal variation in the response of flies to these materials was noted.

Bacteria from uninjured mango fruit were cultured in broth, and such lures gave a rating of 8 as compared with 4.7 for the fermenting sugar solution used as a control. The attraction of cultures of wild yeasts indicated that further studies should be made. Various extracts of host plants were not attractive.

In trap studies on adult activity in mango trees, temperature was found to be the most influential of measured factors on both sexes. Time of day was important in respect to males but not to females. Rate of evaporation was second in importance with the females but of least effect on the males. The attachment of screens of different mesh to exclude moths from the standard glass traps reduced the number of fruitflies captured.

Three females of *Anastrepha ludens* lived as long as 11 months in the laboratory, and a male lived for 14 months. Four flies, all males, were alive in another test at the end of 16 months.

A spray containing nicotine sulfate (40-percent of nicotine) and used at the rate of 1 part in 200 to 300 parts of aqueous solution containing 5 percent of molasses was effective over a long period under conditions of low humidity. Both toxicity and nicotine content fell off rapidly under conditions of high humidity. Toxicity of nicotine sulfate-molasses solutions remained fairly uniform up to about pH. 6.3, but began to drop off rapidly above pH 7. Other nicotine compounds tested included nicotine tannate, nicotine binoxalate, nicotine humate, and nicotine bitartrate. Sprays with concentrations of nicotine sulfate (40 percent of nicotine) ranging from 1:60 to 1:200 and with 5 to 10 percent of blackstrap molasses resulted in some reduction in the number of flies captured in field plots, although the actual control never reached much above 50 percent. The reduction in fly population was greater in plots sprayed with 4 pounds of lead arsenate and 4 percent of blackstrap molasses in 100 gallons of aqueous solution.

Preliminary toxicity tests were made with many compounds.

Saponins were included among compounds found to be especially toxic to fruitflies. Flies died rapidly when exposed to sweetened decoctions of the leaves and stems of *Haplophyton cimicidum.*

Field tests with tartar emetic were carried out, using this compound at the rate of 4 pounds in 100 gallons of solution containing 5 percent of molasses. Trap records showed reductions in fly populations in grapefruit trees as high as 91 percent after applications of sprays containing tartar emetic. Rain, however, often reduced the effectiveness of soluble tartar emetic sprays.

Descriptions are given of fungi found attacking adults of the Mexican fruitfly and related species. Mites are sometimes found in abundance on fruitflies.

Various surveys resulted in more complete knowledge of the habits and distribution of fruitflies in different sections of Mexico.

Nineteen species of fruitflies were segregated and were shown to belong to the genus *Anastrepha* or to related genera. Detailed description is given of the morphology of the ovipositor and the male claspers. The structure of these organs is useful in separating different species and genera.

Anastrepha pallens was shown to differ from species of *Anastrepha* by the structure of the genitalia of the adults and the size, number, and arrangement of the interspiracular processes of the larvae. It was therefore segregated from *Anastrepha* and is now placed in the genus *Pseudodacus.* It attacks the fruits of *Bumelia spiniflora* growing in southern Texas and northeastern Mexico.

An undescribed species to which the name *sagittata* was given was found to differ from species in any of the existing genera, and it was therefore segregated as representing a new genus, along with several other species. It is now known as *Lucumaphila sagittata.* The larvae were found living in the seeds of yellow sapote. At 77° F. the time occupied within the puparium was 32–33 days.

Anastrepha serpentina is important in Mexico because it heavily infests the sapote and related fruits, but at the present time its importance to the United States is less evident. It has been recorded, however, as infesting peach, apple, pear, and quince in northern Mexico. Larvae of this species were reported as infesting oranges in Panama, and in one instance they were found infesting grapefruit in the Rio Grande Valley of Texas. Several wild fruits are also attacked in Mexico. In the laboratory females of *A. serpentina* punctured grapefruit, sweet orange, navel orange, and sweet lime. Grapefruit, California cherries, pear, Natal plum, peach, and pear were infested. Kumquat was infested, but the larvae did not survive, owing to the molding of the fruit. It seems evident that when individual flies of *A. serpentina* lay up to 600 eggs over a relatively short period of time, about a month and a half, most of these are fertile. One female deposited 700 eggs. Adults may live more than a year.

Anastrepha striata is seldom known to attack fruits other than the guava or those very closely related to it. It is a common species throughout the central and southern part of Mexico but is largely replaced by another species, Mexican *A. fraterculus*, in the north.

Anastrepha distincta commonly breeds in pods of *Inga* sp. Mated adults were given access to numerous fruits and other products in the laboratory, and larvae resulted in lima grande, chili pepper, apple, and yellow sapote.

Mexican *Anastrepha mombinpraeoptans* is separated from the true or Puerto Rican *A. mombinpraeoptans* by certain differences in morphology and habits. In Puerto Rico *A. mombinpraeoptans* is a decided pest of mangoes, whereas in Morelos its counterpart rarely if ever attacks mango even when *Spondias* and mango trees grow together. There are also differences between the larvae found in Puerto Rico and in Morelos. The eggs of *A. ludens*, *A. striata*, Mexican *A. mombinpraeoptans*, and *A. serpentina* were differentiated and illustrated. Mexican *A. mombinpraeoptans*, reared in large numbers from *Spondias* sp., was tested for oviposition with a large variety of fruits, but the only fruits infested were fig, yellow mombin, and yellow plum. It was never possible to get mangoes infested in the laboratory. Adults of Mexican *A. mombinpraeoptans* lived in the laboratory for many months, and one individual lived 1 year and 44 days.

Anastrepha fraterculus attacks various fruits, including peach, *Citrus*, guava, *Spondias*, and *Eugenia*, in South America. The form found in Mexico is considered as Mexican *A. fraterculus* because of its different habits and because there are certain morphological differences between it and the South American form. The form attacking guavas, and to some extent peaches, in northern Mexico appears to be the same as the form attacking tropical almond and rose apple in the south, but specific biological studies will have to be made to determine whether northern and southern forms are in all ways identical. Mexican *A. fraterculus* has not been found to attack *Citrus*.

Mexican examples of *Anastrepha chiclayae* reared from maypop (*Passiflora* sp.) differ somewhat from the original form described from Peru, of which the host is unknown.

Anastrepha aphelocentema closely resembles *A. ludens* superficially. It attacks socavite, a fruit apparently belonging to the old genus *Lucuma*. *A. aphelocentema* failed to infest any of a series of fruits which were exposed to mated adults in the laboratory.

Toxotrypana curvicauda is the most common fruitfly found attacking papayas in central and southern Mexico. Specimens captured in traps in Texas and northeastern Mexico differ definitely from typical *T. curvicauda*, and these principally attack a fruit known as talayotillo, or talayote, which grows on a vine and belongs to the milkweed family.

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